PHYTOGEOGRAPHY OF NORTHWESTERN NORTH AMERICA: BRYOPHYTES AND VASCULAR PLANTS

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INTRODUCTION

Within northwestern North America there are a number of fairly natural phytogeographic regions, each characterized by a series of endemic and associated species with common affinities. The present survey does not attempt to discuss all of these regions or to give exhaustive lists of the flora that characterizes them. This study can be considered very preliminary, to be amplified and improved with additional floristic information and of detailed preparation of distribution maps. Those of Hultén (1968) emphasize the importance of such maps.

Subspecific categories are not considered here. Although several species are represented in western North America by endemic subspcies, this is not indicated in the discussion.

In the present discussion the region covered is as follows: Alaska and Yukon, British Columbia and the Rocky Mountains portion of Alberta, and also including the area of Hitchcock, *et al.,* (1955–1969), *Vascular Plants of the Pacific Northwest:* "Washington State, the northern half of Oregon (approximately north of the 44th parallel), Idaho north of the Snake River Plains, the mountainous portion of Montana, and an indefinite southern fringe of British Columbia." For the distribution of the vascular plants, therefore, the basic sources have been Hultén (1968), Hitchcock, *et al.* (1955–1969), Henry (1915), and Eastham (1947). Reference has been made also to the introductory portions of Davis (1952), Peck (1941), Piper (1906), and Calder and Taylor (1968). For the mosses the basic source of distributional data has been Grout (1928–1939), although these data have been considerably expanded. For the hepatics Frye and Clark (1937–1947) and Arnell (1956) have provided general information, greatly amplified by more recent literature.

The region covered is phytogeographically complex. It occupies an area somewhat more than one third the area of Europe. The climate varies from arctic to temperate, from oceanic to continental, from extremely humid to arid. Latitude ranges from north of the Arctic circle (to somewhat beyond 71°N) southward to approximately 44°N, and longtitude from 170°E to approximately 113°E. The elevation ascends from sea-level to 20,320 ft., Mt. McKinley, Alaska, with numerous mountain chains possessing peaks more than 10,000 ft. high. The geologic substrata are equally complex, and widely dispersed through various climatic extremes. Vegetation ranges from arctic and alpine

tundras through boreal coniferous, montane coniferous, humid coastal coniferous and drier coniferous forests, and arid grassland to semi-desert. This is discussed by Daubenmire (1969).

Besides these factors, the present composition of the flora has been moulded by historical circumstances. A major factor determining the present ranges of species was the Pleistocene glaciations and the intervening interglacials. Associated with climatic changes were variations in the position and nature of corridors of migration, thus leading to expansion or restriction of floral boundaries. The flora available preceding the Pleistocene glaciations is discussed by Wolfe and Leopold (1967) and Wolfe (1969).

In Alaska and Yukon there existed, during the Pleistocene glaciations, large unglaciated areas that served as refugia for the flora. This flora consisted largely of circumboreal and circumpolar species, but also possessed taxa surviving from floras of the more distant past, some of them possibly from Tertiary time. These taxa are discussed in detail later. Smaller unglaciated areas existed also in the Queen Charlotte Islands, British Columbia, and possibly at higher elevations in the Rocky Mountains of Canada.

South of the boundary of the continental glaciers, a considerable portion of Idaho, Washington and Oregon has been colonized by plants for many millions of years. Post-Pleistocene and recent variations in the vegetational composition are discussed by Heusser (1960; 1965). Colinvaux (1967) has summarized the Quaternary vegetational history of arctic Alaska.

Phytogeographic examination of the vascular flora of northwestern North America appears to have lagged behind floristic studies. Although Asa Gray (1859) compared the flora of western North America with that of Japan, and Gray and Hooker (1880) analyzed the Rocky Mountain flora, it is Piper (1906) who first attempted to summarize all of the floristic elements. Harshberger (1911) also analyzed floristic elements, but concentrated on floristic composition of the vegetation instead of the ranges of the species that make up the flora. Peck (1941) has also summarized the floristic composition of vegetational areas in Oregon, noting phytogeographic affinities. Weber (1965) has discussed the phytogeography of the southern Rocky Mountains.

Although several studies of the phytogeography of California have appeared (summarized in Stebbins and Major, 1965), the only other major analysis of the total vascular flora of an extensive area in Western North America is that of Cooper (1936) in his analysis of the strand and dune flora of the Pacific coast. Unfortunately Detling did not complete his comprehensive study of the flora of the Pacific Northwest, but fragments of the manuscript have been published (Detling, 1968). Northward, in Alaska, Hultén has published numerous studies, first his beautiful synthetic study (1937) and culminating in his recent *Flora of Alaska and Neighboring Territories* (1968). His atlases of vascular

plant distributions (1958; 1962) have also contributed considerably to the understanding of the ranges of plants in the boreal and arctic portions of the Northern Hemisphere. Another publication of similar significance is that of Meusel, *et al.* (1965). Distribution maps illustrating ranges of arctic and boreal species in Canada have been published by Raup (1947), Raymond (1950), and Porsild (1955; 1957; 1958; 1966), and are particularly important in understanding taxa of circumboreal and circumarctic distribution. In many cases these maps have shown that earlier interpretation of species as disjunct have resulted from inadequate collection. The check-list of Porsild and Cody (1968) adds further such evidence, amplified somewhat in Cody and Porsild (1968).

A general phytogeographic synthesis for the bryoflora has not appeared previously. Herzog (1926) has briefly summarized the affinities of the bryoflora of western North America, with a concentration on endemism. Irmscher (1929) has discussed disjunctions, and makes reference to western North American mosses. The most complete summaries of bryophyte floristic elements are included in Evans (1914), Koch (1954; 1956), Steere (1959; 1965), Persson (1949), Iwatsuki (1958), Schofield (1965; 1968a; 1968b), and Ireland and Schofield (1967). The maps of Szweykowski (1961–1969) are highly important in understanding the distribution of circumboreal hepatics.

In the following discussion the flora is treated initially by major phytogeographic elements. Within each of these, more detailed distributional patterns are considered. In each section hepatics are treated first, followed by mosses and vascular plants. For the bryophytes the order of taxa is basically that of Arnell (1965) for the hepatics, Crum, *et al.* (1965) for the mosses, Hitchcock, *et al.* (1955–1969) for the vascular plants peculiar to the region of that flora and Hultén (1968) for Alaskan and other species of northern distribution.

ENDEMISM

In this category are treated those taxa that are either restricted to the area of the study or extend into it, but are western North American endemics. The latter designation includes taxa that are confined mainly to areas in or west of the Rocky Mountains, infrequently extending eastward in the prairies or, occasionally, to the Black Hills of South Dakota.

Endemic genera

In the bryophytes, although the number of endemic genera is not great, northwestern North America shows greater richness than the remainder of North America, north of Mexico. In the hepatics there is the Family Gyrothyraceae with the genus *Gyrothyra* Howe (Schuster, 1955) which occurs from coastal northern California northward to south coastal Alaska. This taxon has undoubtedly increased in abundance with the increase in disturbance by man. It is particularly abundant on roadside silts and clays.

Endemic moss genera include: *Crumia* Schof., *Roellia* Kindb., *Leucolepis* Lindb., *Pseudobraunia* (Lesq. & James) Broth., *Alsia* Sull., *Dendroalsia* Britt., *Bestia* Broth., *Tripterocladium* (Müll.) Kindb., *Trachybryum* (Broth.) Schof., and *Rhytidiopsis* Broth.

Of these genera *Roellia, Trachybryum,* and *Rhytidiopsis* are confined largely to subalpine elevations, although *Trachybryum* sometimes descends to sea level and is occasionally associated with the oak woodland from northern California to southwestern British Columbia. *Leucolepis* is widespread at all elevations. *Pseudobraunia, Alsia, Dendroalsia, Bestia,* and *Tripterocladium* are predominantly of lower elevations and occur mainly west of the Cascade Mountains. *Crumia* is more widespread (Schofield, 1966), being restricted by its calcareous seepage habitat rather than by elevation. It it noteworthy that all endemic moss genera except *Pseudobraunia* and *Tripterocladium* are dioecious and none possess any special gemmae for vegetative reproduction, yet most show very wide geographic range and often occur in great abundance.

In the vascular flora generic endemism is particularly notable.

Gramineae: *Pleuropogon* R.Br. and *Scribneria* Hack.

Liliaceae: *Camassia* Lindl., *Leucocrinum* Nutt., and *Scoliopus* Torr.

Orchidaceae: *Eburophyton* Heller.

Chenopodiaceae: *Grayia* H. & A., *Nitrophila* Wats., and *Sarcobatus* Nees.

Portulacaceae: *Calyptridium* Nutt., *Lewisia* Pursh, and *Spraguea* Torr.

Berberidaceae: *Vancouveria* Morr. & Dec.

Papaveraceae: *Canbya* Parry, *Eschscholtzia* Cham., and *Meconella* Nutt.

Cruciferae: *Anelsonia* Macbr. & Pays., *Athysanus* Greene, *Caulanthus* Wats., *Chlorocambe* Rydb., *Idahoa* Nels. & Macbr., *Phoenicaulis* Nutt., *Physaria* (Nutt.) Gray, *Polyctenium* Greene, *Schoenocrambe* Greene, *Stanleya* Nutt., *Streptanthella* Rydb., *Thelypodium* Endl., and *Thysanocarpus* Hook.

Sarraceniaceae: *Darlingtonia* Torr.

Saxifragaceae: *Bolandra* Gray, *Conimitella* Rydb., *Elmera* Rydb., *Lithophragma* Nutt., *Peltiphyllum* Engl., *Suksdorfia* Gray, *Telesonix* Raf., *Tellima* R.Br., and *Tolmiea* T. & G.

Hydrangeaceae: *Whipplea* Torr.

Rosaceae: *Chamaebatiaria* (Porter) Maxim., *Kelseya* (Wats.) Rydb., *Luetkea* Bong., *Osmaronia* Greene, *Peraphyllum* Nutt., *Petrophytum* (Nutt.) Rydb., and *Purshia* DC.

Umbelliferae: *Orogenia* Wats., *Perideridia* Reichenb., *Rhysopterus* Coult. & Rose, and *Sphenosciadium* Gray.

Cactaceae: *Pediocactus* Britt. & Rose.

Malvaceae: *Sidalcea* Gray.

Euphorbiaceae: *Eremocarpus* Benth.

Ericaceae: *Allotropa* Torr. & Gray, *Cladothamnus* Bong., *Hemitomes* Gray, *Pityopus* Small, and *Pleuricospora* Gray.

Primulaceae: *Douglasia* Lindb.

Polemoniaceae: *Eriastrum* Woot. & Standl., *Gymnosteris* Greene, *Langloisia* Greene *Leptodactylon* H. & A., and *Linanthastrum* Ewan.

Hydrophyllaceae: *Ellisia* L., *Hesperochiron* Wats., and *Romanzoffia* Cham.

Boraginaceae: *Coldenia* L., and *Dasynotus* Johnst.

Scrophulariaceae: *Chionophila* Benth., *Cordylanthus* Nutt., *Mimetanthe* Greene, *Synthyris* Benth., and *Tonella* Nutt.

Valerianaceae: *Plectritis* DC.

Campanulaceae: *Downingia* Torr., *Githopsis* Nutt., *Heterocodon* Mitt., *Howellia* Gray, and *Porterella* Torr.

Compositae: *Apargidium* T. & G., *Bahia,* Laq., *Balsamorhiza* Nutt., *Blepharipappus* Hook., *Chaenactis* DC., *Chrysothamnus* Nutt., *Crocidium* Hook., *Dimeresia* Gray, *Eatonella* Gray, *Enceliopsis* (Gray) Nels., *Eriophyllum* Laq., *Hulsea* Torr. & Gray, *Luinia* Benth., *Madia* Mol., *Raillardella* Benth., *Rigiopappus* Gray, and *Wyethia* Nutt.

More than half of these genera are monotypic. Many are widespread, *Camassia, Sarcobatus, Eschscholtzia, Lewisia, Romanzoffia, Lithophragma, Luetkea, Apargidium,* etc., where others, *Scribneria, Chlorocambe, Darlingtonia,* etc., are highly restricted in their range. Of particular interest is the fact that there are no endemic genera of Pteridophytes or Gymnosperms. A number of families are especially rich in endemic genera: Cruciferae (13 genera), Saxifragaceae (19 genera), Rosaceae (7 genera) and Compositae (17 genera). Many of these genera are restricted to rather arid regions, although a number are of alpine and subalpine habitats and others are of forests at lower elevations. As in the bryophytes, most of the genera are clearly distinct from related genera.

Since there is such a richness of endemic species, these are treated here in relation to thir distribution pattern in the region.

Species Endemism

Widespread at Elevations Below Subalpine

These species are conspicuous elements of both flora and vegetation. The vascular plants give the vegetation its physiognomic character and the bryophytes tend to dominate that flora in other strata. Within such a wide range many species are environmentally restricted. For example, some bryophytes are consistently on perennially dry and exposed rock surfaces while others are confined to rocks perennially inundated. The forest is entirely of endemic trees and mainly of endemic shrubs, and the herbaceous vegetation is dominated by endemic species. Most of the species do not extend beyond the crests of the Rocky Mountains and many disappear with the boundary to the boreal coniferous forest of northern latitudes or the arid portions of the interior regions. Thus the

widespread element is found in regions of relatively high precipitation on both the coast and lower elevations of the coastal mountains and also at lower elevations of the mountains west of the Rockies. Many of the species extend southward along the coast as far south as the southern limits of the coastal redwood forest (*Sequoia sempervirens* (Don) Endl.) in California and occasionally at lower elevations of the Sierra Nevada.

Within this same geographic area are other floristic elements; these are discussed elsewhere in this paper. Their phytogeographic significance is great, but their contribution to the vegetational cover is generally smaller than that of the endemic species, particularly in the vascular flora.

The distributions of the hepatics are not well understood since collection has been rather limited: *Gyrothyra underwoodiana* Howe., *Plectocolea rubra* (Gottsche) Evans, *Scapania americana* Müll., *Bazzania ambigua* (Lindenb.) Trevis., *Radula bolanderi* Gottsche, *Porella roellii* Steph., *P. navicularis* (Lehm. & Lindenb.) Lindb., *Frullania nisquallensis* Sull., and *F. franciscana* Howe.

Among the mosses the details are somewhat clearer and the representation of endemic taxa is somewhat greater: *Sphagnum mendocinum* Sull. & Lesq., *Atrichum selwynii* Aust., *Pogonatum macounii* (Kindb.) Kindb. & Mac., *Ditrichum ambiguum* Best, *D. schimperi* (Lesq.) Kunze, *Dicranella* n. sp., *Amphidium californicum* (Hampe) Broth., *Dicranum howellii* Ren. & Card., *Barbula rubiginosa* Mitt., *Scouleria aquatica* Hook., *Racomitrium depressum* Lesq., *R. varium* (Mitt.) Lesq. & James, *Pohlia longibracteata* Broth., *Leucolepis menziesii* (Hook.) Steere, *Plagiomnium insigne* (Mitt.) Koponen, *P. venustum* (Mitt.) Koponen, *Rhizomnium glabrescens* (Kindb.) Koponen, *Ulota megalospora* Vent., *U. obtusiuscula* Müll. & Kindb., *Orthotrichum consimile* Mitt., *Fontinalis neomexicana* Sull. & Lesq., *F. patula* Card., *Dichelyma uncinatum* Mitt., *Neckera douglasii* Hook., *Porotrichum bigelovii* (Sull.) Kindb., *Thamnobryum leibergii* (Britt.) Nieuwl., *Isothecium stoloniferum* (Hook.) Brid., *Claopodium bolanderi* Best, *Homalothecium fulgescens* (Mitt.) Lawt. *Brachythecium frigidum* (Müll.) Besch., B. *lamprochryseum* Müll. & Kindb., *Eurhynchium oreganum* (Sull.) Jaeg. & Sauerb., *Scleropodium obtusifolium* (Hook.) Kindb., and *Hypnum circinale* Hook.

These bryophytes occupy a diversity of habitats but the majority are epiphytic on tree trunks and occur less commonly on rock. The remainder occupy various habitats, from splashed rock faces, for example *Scouleria aquatica* and *Scleropodium obtusifolium;* humid cliff bases, on rock or on soil, *Pogonatum macounii, Pohlia longibracteata, Porotrichum bigelovii,* and *Thamnobryum leibergii;* rotten logs or forest floor, *Dicranum howellii* and *Brachythecium frigidum;* or aquatic *Sphagnum mendocinum* and *Fontinalis neomexicana.*

A number of species that have a wide range but are rare are:

Hepatics: *Blepharostoma arachnoideum* Howe, *Jungermannia allenii* Clark, *Plectocolea rubra* (Gottsche.) Evans, and *Sphaerocarpos hians* Haynes.

Mosses: *Fissidens ventricosus* Lesq., *F. pauperculus* Howe, *Crumia latifolia* (Kindb.) Schof., *Scouleria marginata* Britt., *Brotherella roellii* (Ren. & Card.) Fleisch., and *Triperocladium leucocladulum* (Müll.) Kindb.

Based on their present ecology and distribution it can be inferred that during glaciation, the bulk of these species persisted largely south of the glacial boundary, probably in forested environments. The relative scarcity of most of them in unglaciated Alaska indicates that they did not persist there. A number of these species have probably increased in abundance in recent times, largely with the expansion of the available habitat, chief among these are *Gyrothyra underwoodiana,* an undescribed *Dicranella,* and *Pohlia longibracteata,* all of which frequently abound on moist road-cuts. Many others have probably been greatly restricted by the elimination of their forest habitat, although gross distributional pattern probably has not been greatly altered.

The vascular flora of this widespread distribution is large. The woody elements of this flora characterize the vegetation. Since these taxa are endemic, the impression of great endemism results in spite of the very considerable number of circumboreal and circumpolar species that make up the total flora. The following list is far from complete, but will serve to illustrate the diversity of taxa present:

Polypodiaceae: *Polystichum munitum* (Kaulf.) Presl, *Polypodium glycyrhiza* Eat., and *P. hesperium* Maxon.

Taxaceae: *Taxus brevifolia* Nutt.

Pinaceae: *Pinus contorta* Dougl., *Picea sitchensis* (Bong.) Carr., *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Abies grandis* (Dougl.) Lindl.

Cupressaceae: *Chamaecyparis nootkatensis* (Lamb.) Spach.

Juncaceae: *Juncus brachyphyllus* Wieg. and *J. oreganus* Wats.

Liliaceae: *Clintonia uniflora* (Schult.) Kunth, *Disporum hookeri* (Torr.) Nichols, *Erythronium oreganum* Appleg., *E. revolutum* Sm., *Trillium ovatum* Pursh, *Veratrum californicum* Durand, and *Zygadenus elegans* Pursh.

Orchidaceae: *Cypripedium montanum* Dougl. and *Listera caurina* Piper.

Poaceae: *Agropyron spicatum* (Pursh.) Scribn. & Sm., *Agrostis aequivalvis* Trin., *A. diegoensis* Vasey, *A. idahoensis* Nash., *A. microphylla* Steud., *Bromus pacificus* Shear, *Elymus innovatus* Beal, *Festuca idahoensis* Elmer, *F. subulata* Trin., *Glyceria elata* (Nash.) Hitchc., *Melica subulata* (Griseb.) Scribn., *Poa laxiflora* Buckl., *P. stenantha* Trin., and *Trisetum cernuum* Trin.

Cyperaceae: *Carex atrostachya* Olney, *C. preslii* Steud., *C. phaeocephala* Piper, *C. petasata* Desv., *C. microptera* Mack., *C. laeviculmis* Meinsch., *C. phyllomanica* Boott., *C. scopulorum* Holm, *C. kelloggii* Boott., and *C. sitchensis* Prescott.

Araceae: *Lysichiton americanum* Hult. & St. John.

Salicaceae: *Salix lasiandra* Benth., *S. scouleriana* Benth., and *S. sitchensis* Sanson.

Betulaceae: *Alnus rhombifolia* Nutt. and *A. rubra* Bong.

Aristolochiaceae: *Asarum caudatum* Lindl.

Portulacaceae: *Montia parvifolia* (Moc.) Greene and *M. sibirica* (L.) Howell.

Caryophyllaceae: *Silene menziesii* Hook.

Ranunculaceae: *Aconitum columbianum* Nutt., *Aquilegia formosa* Fisch., *Coptis asplenifolia* Salisb., *Ranunculus alismaefolius* Geyer, *R. occidentalis* Nutt., and *Thalictrum occidentale* Gray.

Berberidaceae: *Berberis aquifolium* Pursh.

Saxifragaceae: *Boykinia elata* (Nutt.) Greene, *Heuchera cylindria* Dougl., *H. glabra* Willd., *H. micrantha* Dougl., *Mitella trifida* Grah., *Saxifraga ferruginea* Grah., *Tellima grandiflora* (Pursh.) Dougl., *Tiarella trifoliata* L., *Tolmiea menziesii* (Pursh.) T. & G., *Ribes bracteosum* Dougl., and *R. laxiflorum* Pursh.

Rosaceae: *Holodiscus discolor* (Pursh.) Maxim., *Osmaronia cerasiformis* (T. & G.) Greene, *Physocarpus capitatus* (Pursh.) Kuntze, *Potentilla glandulosa* Lindl., *P. gracilis* Dougl., *Prunus emaginata* (Dougl.) Walpers, *Pyrus fusca* Raf., *Rosa gymnocarpa* Nutt., *R. nutkana* Presl., *Rubus lasiococcus* Gray, *R. leucodermis* Dougl., *R. nivalis* Dougl., and *Spiraea douglasii* Hook.

Leguminosae: *Lathyrus nevadensis* Wats., *Lotus purshianus* (Benth.) Clements & Clements, *Lupinus lepidus* Dougl., and *L. polyphyllus* Lindl.

Oxalidaceae: *Oxalis oregana* Nutt.

Celastraceae: *Pachystima mysinites* (Pursh) Raf.

Aceraceae: *Acer circinatum* Pursh and *A. glabrum* Torr.

Balsaminiaceae: *Impatiens ecalcarata* Blank.

Rhamnaceae: *Ceanothus sanguineus* Pursh and *Rhamnus purshiana* DC.

Hypericaceae: *Hypericum anagalloides* C. & S.

Violaceae: *Viola purpurea* Kell.

Onagraceae: *Boisduvalia densiflora* (Lindl.) Wats., *Epilobium glaberrimum* Barbey, *E. luteum* Pursh, and *E. minutum* Lindl.

Cornaceae: *Cornus nuttallii* Aud.

Ericaceae: *Allotropa virgata* T. & G., *Chimaphila menziesii* (R.Br.) Spreng., *Gaultheria shallon* Pursh, *Menziesia ferruginea* Sm., *Pleuricospora fimbriolata* Gray, *Pyrola aphylla* Sm., *P. dentata* Sm., *P. picta* Sm., *Vaccinium alaskaense* Howell, and *V. parvifolium* Sm.

Primulaceae: *Dodecatheon jeffreyi* van Houtte.

Gentianaceae: *Gentiana sceptrum* Griseb. and *G. douglasiana* Bong.
Convolvulaceae: *Cuscuta occidentalis* Millspaugh.
Hydrophyllaceae: *Romanzoffia sitchensis* Bong.
Caprifoliaceae: *Lonicera ciliosa* (Pursh) DC.
Campanulaceae: *Heterocodon rariflorum* Nutt.
Compositae: *Agoseris grandiflora* (Nutt.) Greene, *Antennaria anaphaloides,* Rydb., *A. corymbosa* Nels., *A. dimorpha* (Nutt.) T. & G., *Arnica amplexicaulis* Nutt., *A. diversifolia* Greene, *A. latifolia* Bong., *Aster subspicatus* Nees, *Microseris laciniata* (Hook.) Schultz-Bip., and *Prenanthes alata* (Hook.) Dietr.

Subalpine and Alpine

Besides possessing a flora containing rich representation of circumpolar species, the mountains of northwestern North America have many bryophyte and vascular plant endemics. The woody flora is essentially endemic but not confined to the mountains while endemism decreases in the herbs and bryophytes. The subalpine forest probably possesses more endemic bryophytes than the alpine portion, but in the vascular flora endemism increases in alpine areas. While some mountains serve as islands of endemism for vascular plants, the bryophytes are not so confined. This is in spite of very narrow environment restriction of many of them. Most of these bryophytes produce numerous sporophytes annually although several are dioicous. Special vegetative reproductive organs are not known for any of the endemic alpine bryophytes.

In the following discussion the widespread subalpine and alpine species are treated first and various mountains are noted with their endemic floras.

1. Widespread subalpine and alpine

Hepatics: *Macrodiplophyllum imbricatum* (Howe) Perss.

Mosses: *Oligotrichum parallelum* (Mitt.) Kindb., *Polytrichadelphus lyallii* Mitt., *Buxbaumia piperi* Best, *Ditrichum montanum* Leib., *Trematodon boasii* Schof., *Dicranoweisia roellii* Kindb., *Dicranum pallidisetum* (Bailey) Irel., *Grimmia atricha* Müll. & Kindb., *Pohlia columbica* (Kindb.) Andr., *Roellia roellii* (Broth.) Crum, *Lescuraea baileyi* (Best & Grout) Lawt., *L. atricha* (Kindb.) Lawt., *L. stenophylla* (Ren. & Card.) Kindb., *Heterocladium procurrens* (Mitt.) Rau. & Herv., *Hygrohypnum bestii* (Ren. & Bryhn.) Holz., *Trachybryum megaptilum* (Sull.) Schof., *Brachythecium leibergii* Grout, *B. hylotapetum* Hig. & Hig., and *Rhytidiopsis robusta* (Hook.) Broth.

Vascular Plants:
Polypodiaceae: *Pellaea bridgesii* Hook.
Pinaceae: *Larix occidentalis* Nutt., *L. lyallii* Parl., *Pinus albicaulis* Engelm., *P. flexilis* James, *P. monticola* Dougl., *Tsuga mertensiana*

(Bong.) Sarg., *Abies amabilis* (Dougl.) Forbes, *A. lasiocarpa* (Hook.) Nutt., and *Picea engelmannii* Parry.

Cupressaceae: *Juniperus occidentalis* Hook.

Juncaceae: *Juncus drummondii* Mey., *J. mertensianus* Bong., *J. parryi* Engelm., and *J. regelii* Buch.

Cyperaceae: *Carex anthoxanthea* Presl., *C. circinnata* Mey., *C. nigricans* Mey., *C. albonigra* Mack., *C. atrata* L., *C. mertensii* Prescott, and *C. petricosa* Desv.

Liliaceae: *Allium validum* Wats., *Erythronium grandiflorum* Pursh, *E. montanum* Wats., *Lilium columbianum* Hanson, *Stenanthium occidentale* Gray, and *Xerophyllum tenax* (Pursh) Nutt.

Orchidaceae: *Cypripedium montanum* Dougl.

Poaceae: *Agrostis humilis* Vasey, *A. thurberiana* Hitchc., *A. variabilis* Rydb., *Bromus sitchensis* Trin., *B. suksdorfii* Vasey, *Calamagrostis tweedyi* (Scribn.) Scribn., *Festuca viridula* Vasey, *Melica spectabilis* Scribn., *Oryzopsis exigua* Thurb., *Poa bolanderi* Vasey, *P. curta* Rydb., *P. curtifolia* Scribn., *P. gracillima* Vasey, *P. grayana* Vasey, *P. lettermanii* Vasey, *P. nervosa* (Hock.) Vasey, *P. reflexa* Vasey & Scribn., and *P. suksdorfii* (Beal) Vasey.

Salicaceae: *Salix barclayi* Anderss., *S. barrattiana* Hook., *S. cascadensis* Cockerell, *S. dodgeana* Rydb., *S. geyeriana* Anderss., *S. nivalis* Hook., *S. tweedyi* (Bebb) Ball, and *S. wolfii* Bebb.

Polygonaceae: *Eriogonum androsaceum* Benth., *E. chrysops* Rydb., *E. pyrolifolium* Hook., *Polygonum bistortoides* Pursh, *P. minimum* Wats., *P. newberryi* Small, *P. phytolaccifolium* Meisn., and *Rumex paucifolius* Nutt.

Caryophyllaceae: *Silene parryi* (Wats.) Hitchc. & Maguire, *S. scaposa* Robins., *S. scouleri* Hook., and *Stellaria jamesiana* Torr.

Ranunculaceae: *Aquilegia jonesii* Parry, *Caltha biflora* D.C., *C. leptosepala* D.C., *Delphinium glareosum* Greene, *D. glaucum* Wats., *D. occidentale* Wats., *Ranunculus cardiophyllus* Hook., *R. cooleyae* Vasey & Rose, *R. eschscholtzii* Schlecht., *R. inamoenus* Greene, and *R. verecundus* Robins.

Papaveraceae: *Papaver pygmaeum* Rydb.

Fumariaceae: *Dicentra uniflora* Kell.

Cruciferae: *Anelsonia eurycarpa* (Gray) Macbr. & Pays., *Arabis furcata* Wats., *A. lyallii* Wats., *A. microphylla* Nutt., *A. platyperma* Gray, *Cardamine breweri* Wats., *Chlorocrambe hastata* (Wats.) Rydb., *Draba apiculata* Hitchc., *D. aurea* Vahl., *D. crassifolia* Nutt., *D. densifolia* Nutt., *D. incerta* Pays., *D. lonchocarpa* Rydb., *D. paysonii* Macbr., *D. praealta* Greene, *D. stenoloba* Ledeb., and *D. ventosa* Gray.

Crassulaceae: *Sedum oregonense* (Wats.) Peck.

Saxifragaceae: *Elmera racemosa* (Wats.) Rydb., *Leptarrhena pyrolifolia* (Don) R. Br., *Mitella breweri* Gray, *Parnassia fimbriata* Konig., *Saxifraga arguta* Don, *S. chrysantha* Gray, *S. debilis* Engelm., *S. occi-*

dentalis Wats., *S. oregana* Howell, *S. tolmiei* T. & G., *Telesonix jamesii* (Torr.) Raf., *Ribes howellii* Greene, *R. mogoelonicum* Greene, and *R. montigenum* McClatchie.

Rosaceae: *Ivesia gordoni* (Hook.) T. & G., *I. tweedyi* Rydb., *Kelseya uniflora* (Wats.) Rydb., *Luetkea pectinata* (Pursh) Kuntze, *Potentilla brevifolia* Nutt., *P. drummondii* Lehm., *P. flabellifolia* Hook., *P. hookeriana* Lehm., *Rubus pedatus* Sm., *Sanguisorba sitchensis* Meyer, and *Spiraea densiflora* Nutt.

Leguminosae: *Astragalus cottonii* Jones, *A. tegetarius* Wats., *A. whitneyi* Gray, *Hedysarum occidentale* Greene, *Oxytropis parryi* Gray, *Trifolium beckwithii* Brew., *T. dasyphyllum* T. & G., *T. nanum* Torr., and *T. parryi* Gray.

Haloragidaceae: *Hippuris montana* Ledeb.

Umbelliferae: *Angelica roseana* Henderson.

Ericaceae: *Cassiope mertensiana* (Bong.) Don, *Gaultheria humifusa* (Grah.) Rydb., *G. ovatifolia* Gray, *Phyllodoce empetriformis* (Sw.) Don, *Rhododendron albiflorum* Hook., and *Vaccinium membranaceum* Dougl.

Gentianaceae: *Gentiana calycosa* Griseb.

Polemoniaceae: *Polemonium elegans* Greene.

Boraginaceae: *Cryptantha nubigena* (Greene) Pays.

Scrophulariaceae: *Castilleja applegatei* Fern., *C. parviflora* Bong., *C. rhexifolia* Rydb., *Mimulus lewisii* Pursh, *Pedicularis bracteosa* Benth., *P. contorta* Benth., *P. cystopteridifolia* Rydb., *P. ornithorhyncha* Benth., and *Pentstemon davidsonii* Greene.

Valerianaceae: *Valeriana acutiloba* Rydb.

Compositae: *Antennaria lanata* (Hook.) Greene, *A. mollis* Hook., *A. nevadensis* Gray, *Arnica michauxiana* Bess., *A. scopulorum* Gray, *A. alpigenus* (T. & G.) Gray, *Chaenactis alpina* (Gray) Jones, *Erigeron asperugineus* (Eat.) Gray, *E. lanatus* Hook., *E. leiomerus* Gray, *E. simplex* Greene, *E. ursinus* D. C. Eat., *E. vagus* Payson, *Haplopappus lyallii* Gray, *H. pygmaeus* (T. & G.) Gray, *Hulsea algida* Gray, *Saussurea americana* Eat., *Senecio megacephalus* Nutt., *S. subnudus* DC., and *S. werneriifolius* Gray.

2. A number of mountain areas posses their endemic species

a. Rocky Mountains (mainly)

Vascular Plants: *Juncus hallii* Engelm., *J. tweedyi* Rydb., *Allium brevistylum* Wats., *Draba crassa* Rydb., *Sedum debile* Wats., *Conimitella williamsii* (Eat.) Rydb., *Trifolium haydenii* Porter, *Primula parryi* Gray, *Phacelia lyallii* (Gray) Rydb., *Synthyris canbyi* Pennell, *Cirsium tweedyi* Rydb., *Erigeron pallens* Cronq., *Hymenoxys grandiflora* (T. & G.) Parker, and *Townsendia spathulata* Nutt.

b. Cascade Mountains (principally)

Mosses: *Pohlia cardotii* (Ren.) Broth.

Vascular Plants: *Silene suksdorfii* Robins., *Draba aureola* Wats.,

Physaria alpestris Suksd., *Smelowskia ovalis* Jones, *Tauschia stricklandii* (Coult. & Rose) Math. & Const., *Castilleja cryptantha* Greenm., *C. rupicola* Piper, *C. suksdorfii* Gray, *Pedicularis rainierensis* Pennell & Warren, *Aster gormanii* (Piper) Blake, *Erigeron cascadensis* Heller, *Hulsea nana* Gray, *Luinia nardosmia* (Gray) Cronq. and *L. stricta* (Greene) Rob.

c. Olympic Mountains

Vascular Plants: *Petrophytum hendersonii* (Canby) Rydb., *Viola flettii* Piper, *Campanula piperi* Howell, *Aster paucicapitatus* Rob., *Erigeron flettii* Jones, and *Senecio websteri* Greenm.

d. Cascade Mountains, Coast and Insular Mountains, and Olympic Mountains

Mosses: *Dichodontium olympicum* Ren. & Card. and *Grimmia olympica* Britt.

Vascular Plants: *Delphinium glareosum* Greene, *Erysimum arenicola* Wats., *Smelowskia divergens* Wats., *Vaccinium deliciosum* Piper, *Arnica nevadensis* Gray, and *Senecio flettii* Wieg.

e. Wenatchee Mountains

Vascular Plants: *Silene seelyi* Morton & Thompson, *Delphinium viridescens* Leiberg, *D. xantholeucum* Piper, *Lomatium cuspidatum* Math. & Const., *Valeriana columbiana* Piper, *Chaenactis ramosa* Stockwell, and *C. thompsonii* Cronq.

f. Wallowa Mountains (sometimes also in Blue Mountains)

Vascular Plants: *Lomatium greenmanii* Mathias, *L. oreganum* Coult. & Rose, *Castilleja chrysantha* Greenm., *C. fraterna* Greenm., *C. glandulifera* Pennell, *C. owenbeyana* Pennell, *C. rubida* Piper, *Pentstemon spathulatus* Pennell, and *Senecio porteri* Greene.

There are numerous other subalpine and alpine endemics, in a number of cases of very restricted distribution. The majority of the endemics are of circumpolar genera and many are especially rich in species, for example, *Salix, Arabis, Draba, Saxifraga, Trifolium, Castilleja, Pedicularis, Erigeron,* and *Senecio.* Although many of these genera are notoriously polymorphic, the endemic species tend to be remarkably distinct. Since many of the species are ecologically restricted, their discovery is often by chance, and thus their total distribution through mountainous western North America is not thoroughly known. Considerable botanical exploration even in presumably well-known mountain areas, remains to be done.

Dry Interior Plans

East of the Cascade and Coastal Mountains and west of the Rocky Mountains there extends a lowland trough lying in the rain shadow of the coastward mountains. This drier region possesses a vegetation that

is composed predominantly of species endemic to western North America. Many range southward into the cold deserts and some even to the warmer arid regions as far south as Mexico. Many are found also east of the Rocky mountains and the northern limits are largely in central British Columbia, although occasionally some species extend into Yukon and Alaska. Endemism is highest in perennial herbs although some are woody or annual. No endemic hepatics have been reported and few mosses, although little careful bryological exploration has been made in this area.

Bryophytes: *Barbula andreaeoides* Kindb., *B. platyneura* Müll. & Kindb., *Pottia nevadensis* Card. & Thér., *Grimmia calyptrata* Hook., *Funaria americana* Lindb., and *Orthotrichum hallii* Sull. & Lesq.

Vascular Plants

Pinaceae: *Pinus ponderosa* Dougl. and *P. flexilis* James.

Lilliaceae: *Allium nevadense* Wats. *Fritillaria pudica* (Pursh) Spreng., and *Leucocrinum montanum* Nutt.

Iridaceae: *Iris chrysophylla* Howell and *Calochortus bruneaunis* Nels. & Macbr.

Poaceae: *Danthonia parryi* Scribn., *D. unispicata* Munro, *Melica bulbosa* Geyer, *M. fugax* Boland., *Muhlenbergia andina* (Nutt.) Hitchc., *Stipa lettermanii* Vasey, *S. thurberiana* Piper, and *Trisetum wolfii* Vasey.

Ulmaceae: *Celtis douglasii* Planch.

Polygonaceae: *Chorizanthe brevicornu* Torr., *C. watsoni* T. & G., *Eriogonum angulosum* Benth., *E. caespitosum* Nutt., *E. cernuum* Nutt., *E. chrysocephalum* Gray, *E. deflexum* Torr., *E. douglasii* Benth., *E. elatum* Dougl., *E. heracleoides* Nutt., *E. microthecum* Nutt., *E. niveum* Dougl., *E. sphaerocephalum* Dougl., *E. thymoides* Benth., and *Polygonum austiniae* Greene.

Chenopodiaceae: *Atriplex truncata* (Torr.) Gray, *Grayia spinosa* (Hook.) Moq., *Kochia americana* Wats., *Monolepis pusilla* Torr., *M. spathulata* Gray, *Nitrophila occidentalis* (Moq.) Wats., *Salicornia rubra* Nels., *Sarcobatus vermiculatus* (Hook.) Torr., *Suaeda intermedia* Wats., and *S. spaldingii* Wats.

Amaranthaceae: *Amaranthus californicus* (Moq.) Wats.

Portulacaceae: *Calyptridium roseum* Wats., *Lewisia rediviva* Pursh, and *Talinum spinescens* Torr.

Caryophyllaceae: *Arenaria aculeata* Wats., *A. franklinii* Dougl., *A. hookeri* Nutt., *A. pusilla* Wats., *Silene douglasii* Hook., *S. oregana* Wats., and *S. spaldingii* Wats.

Paeoniaceae: *Paeonia brownii* Dougl.

Ranunculaceae: *Clematis hirsutissima* Pursh, *C. ligusticifolia* Nutt., *Delphinium andersonii* Gray, *D. depauperatum* Nutt., *D. glaucescens* Rydb., *D. multiplex* (Ewan) Hitchc., *D. stachydeum* (Gray) Nels. & Macbr., *Myosurus aristatus* Benth., *Ranunculus andersonii* Gray, *R. jovis* Nels., and *R. reconditus* Nels. & Macbr.

Papaveraceae: *Canbya aurea* Wats.

Cruciferae: *Arabis cobrensis* Jones, *A. cusickii* Wats., *A. lignifera* Nels., *Caulanthus crassicaulis* (Torr.) Wats., *C. pilosus* Wats., *Draba douglasii* Gray, *Erysimum occidentale* (Wats.) Robins., *Idahoa scapigera* (Hook.) Nels. & Macbr., *Lepidium dictyotum* Gray, *Lesquerella douglasii* Wats., *L. kingii* Wats., *Phoenicaulis cheiranthoides* Nutt., *Physaria didymocarpa* (Hook.) Gray, *Polyctenium fremontii* (Wats.) Greene, *Schoenocrambe linifolia* (Nutt.) Greene, *Stanleya tomentosa* Parry, S. *viridifolia* Nutt., *Streptanthella longirostris* (Wats.) Rydb., *Thelypodium integrifolium* (Nutt.) Endl., and *T. sagittatum* (Nutt.) Endl.

Saxifragaceae: *Lithophragma parviflora* (Hook.) Nutt., *L. tenella* Nutt., *Ribes aureum* Pursh, and *R. velutinum* Greene.

Rosaceae: *Cercocarpus ledifolius* Nutt., *Chamaebatiaria millefolium* (Torr.) Maxim., *Holodiscus dumosus* (Hook.) Heller, *Peraphyllum ramosissimum* Nutt., and *Purshia tridentata* (Pursh) D.C.

Leguminosae: *Astragalus adanus* Nels., *A. argophyllus* Nutt., *A. arthurii* Jones, *A. atratus* Wats., *A. calycosus* Torr., *A. casei* Gray, *A. cibarius* Sheld., *A. collinus* Dougl., *A. convallarius* Greene, *A. curvicarpus* (Sheld.) Macbr., *A. cusickii* Gray, *A. filipes* Torr., *A. geyeri* Gray, *A. howellii* Gray, *A. inflexus* Dougl., *A. leibergii* Jones, *A. lyallii* Gray, *A. malacus* Gray, *A. microcystis* Gray, *A. newberryi* Gray, *A. nudisiliquus* Nels., *A. obscurus* Wats., *A. palousensis* Porter, *A. reventus* Gray, *A. salmonis* Jones, *A. scaphoides* Jones, *A. sinuatus* Piper, *A. spaldingii* Gray, *A. speirocarpus* Gray, *A. stenophyllus* T. & G., *A. succumbens* Dougl., *A. tegetarioides* Jones, *A. toanus* Jones, *A. tweedyi* Canby, *A. umbraticus* Sheld., *Lathyrus lanszwertii* Kell., *L. pauciflorus* Fern., *L. rigidus* White, *Lupinus caudatus* Kell., *L. holosericeus* Nutt., *L. laxiflorus* Dougl., *L. sabinii* Dougl., *L. saxosus* Howell, *L. wyethii* Wats., *Oxytropis lagopus* Nutt., *Petalostemon ornatum* Dougl., *Trifolium gymnocarpon* Nutt., *T. macrocephalum* Pursh, and *T. thompsonii* Morton.

Malvaceae: *Iliamna longisepala* (Torr.) Wiggins, *Sidalcea neomexicana* Gray, *S. oregana* (Nutt.) Gray, *Sphaeralcea grossulariifolia* (H. & A.) Rydb., and *S. munroana* (Dougl.) Spach.

Violaceae: *Viola beckwithii* T. & G. and *V. trinervata* Howell.

Loasaceae: *Mentzelia albicaulis* Dougl., *M. dispersa* Wats., and *M. laevicaulis* (Dougl.) T. & G.

Cactaceae: *Pediocactus simpsonii* (Engelm.) Britt. & Rose.

Onagraceae: *Oenethera alyssoides* H. & A., *O. andina* Nutt., *O. boothii* Dougl., *O. claviformis* Torr. & Frem., *O. deltoides* Torr. & Frem., *O. minor* (Nels.) Munz, *O. palmeri* Wats., *O. scapoidea* Nutt., and *O. tanacetifolia* T. & G.

Umbelliferae: *Lomatium canbyi* Coult. & Rose, *L. farinosum* (Hook.) Coult. & Rose, *L. gormanii* (Howell) Coult. & Rose, *L. hambleniae* Math. & Const., *L. nudicaule* (Pursh) Coult. & Rose, *L. watsonii* Coult. & Rose, and *Tauschia hooveri* Math. & Const.

Gentianaceae: *Frasera montana* Mulford.

Polemoniaceae: *Gilia minutiflora* Benth., *Gymnosteris nudicaulis* (H. & A.) Greene, *G. parvula* Heller, *Linanthus pharnaceoides* (Benth.) Greene, *Phlox aculeata* Nels., and *P. caespitosa* Nutt.

Hydrophyllaceae: *Hesperochiron californicus* (Benth.) Wats., *Nama aretioides* (H. & A.) Brand, *N. densum* Lemmon, and *Phacelia bicolor* Torr.

Boraginaceae: *P. glandulifera* Piper, *Cryptantha scoparia* Nels., *C. simulans* Greene, *Hackelia arida* (Piper) Johnst., *H. ciliata* (Dougl.) Johnst., *H. patens* (Nutt.) Johnst., *Pectocarya setosa* Gray, and *Plagiobothrys harknessii* (Greene) Nels & Macbr.

Scrophulariaceae: *Castilleja angustifolia* (Nutt.) Don, *C. cervina* Greenm., *C. chromosa* Nels., *C. exilis* Nels., *C. flava* Wats., *C. inverta* (Nels. & Macbr.) Pennell & Ownbey, *C. linariifolia* Benth., *C. longispica* Nels., *C. lutescens* (Greenm.) Rydb., *C. oresbia* Greenm., *C. pallescens* (Gray) Greenm., *C. rustica* Piper, *C. thompsonii* Pennell, *C. xanthotricha* Pennell, *Cordylanthus capitatus* Nutt., *C. ramosus* Nutt., *Mimulus cusickii* (Greene) Piper, *Orthocarpus barbatus* Cotton, *Pentstemon acuminatus* Dougl., *P. barrettiae* Gray, *P. cinicola* Keck, *P. cusickii* Gray, *P. cyaneus* Pennell, *P. gairdneri* Hook., *P. humilis* Nutt., *P. laetus* Gray, *P. lemhiensis* (Keck) Keck & Cronq., *P. peckii* Pennell, *P. pumilus* Nutt., *P. radicosus* Nels., *P. rydbergii* Nels., *P. seorsus* (Nels.) Keck, and *P. speciosus* Dougl.

Orobanchaceae: *Orobanche californica* S. & S.

Compositae: *Antennaria geyeri* Gray, *Artemisia tridentata* Nutt., *A. tripartita* Rydb., *Brickellia microphylla* (Nutt.) Gray, *B. oblongifolia* Nutt., *Cirsium magnificum* (Nels.) Petr., *C. utahense* Petr., *Eatonella nivea* (Eat.) Gray, *Erigeron aphanactis* (Gray) Greene, *E. chrysopsidis* Gray, *E. linearis* (Hook.) Piper, *E. piperianus* Cronq., *E. poliospermus* Gray, *Haplopappus stenophyllus* Gray, *Madia minima* (Gray) Keck, *Rigiopappus leptocladus* Gray, *Stephanomeria exigua* Nutt., and *S. lactucina* Gray.

Californian

A distinctive element in the flora of southwestern British Columbia occupies the so-called "Mediterranean" climatic portion of Southern Vancouver Island, the islands of the southern Strait of Georgia and the headlands of the adjacent mainland. The species occupy sites that are edaphically similar to those occupied by the same taxa further south to California in more conspicuously Mediterranean climates, and where they are more widespread. All species are restricted to west of the Cascade Mountains, occupy drier sites, but are not maritime. This element possibly extended its range northward from California or Oregon to southern British Columbia during the Hypsithermal Interval and fragments persist only in edaphically suitable sites although the general climate of the region is unfavourable.

It is equally possible that the species have entered the region by expanding their range stepwise via the available edaphically suitable sites, and no Hypsithermal Interval need be involved as an initiating cause. The element is conspicuous both in the bryoflora and vascular flora and is represented by both western North American endemics and by species of wider world distribution, but whose restriction is essentially to Mediterranean climates. This element is discussed briefly by Schofield (1965; 1968a; 1968b), and Ireland and Schofield (1967).

Hepatics: *Fossombronia longiseta* Aust. and *Frullania californica* (Aust.) Evans.

Hornworts: *Anthoceros hallii* Aust.

Mosses: *Fissidens ventricosus* Lesq., *Ditrichum ambiguum* Best, *Pleuridium bolanderi* Müll., *Timmiella crassinervis* (Hampe) Koch, *Tortula amplexa* (Lesq.) Steere, *T. bolanderi* (Lesq.) Howe, *Physcomitrium megalocarpum* Kindb., *Ptychomitrium gardneri* Lesq., *Orthotrichum papillosum* Hampe, *Pseudobraunia californica* (Lesq.) Broth., *Alsia californica* (Hook. & Arnott.) Sull., *Dendroalsia abietina* (Hook.) Britt., *Bestia vancouveriensis* (Kindb.) Wijk. & Marg., *Isothecium cristatum* (Hampe) Robins., *Homalothecium nuttallii* (Wils.) Jaeg. & Sauerb., *H. pinnatifidum* (Sull. & Lesq.) Lawt., and *H. arenarium* (Lesq.) Lawt.

Vascular Plants: *Carex brevicaulis* Mack., *Juncus bolanderi* Engelm., *Brodiaea congesta* Smith, *Allium crenulatum* Wieg., *Disporum smithii* (Hook.) Piper, *Erythronium oreganum* Appleg., *E. revolutum* Smith, *Sisyrinchium douglasii* Dietr., *Habenaria elegans* Lindl., *Poa confinis* Vasey, *Quercus garryana* Dougl., *Montia diffusa* (Nutt.) Greene, *Delphinium menziesii* D.C., *Ranunculus lobbii* (Hiern) Gray, *Berberis nervosa* Pursh, *Meconella oregana* Nutt., *Corydalis scouleri* Hook., *Ribes sanguineum* Pursh, *Rosa pisocarpa* Gray, *Lotus micranthus* Benth., *Lupinus bicolor* Lindl., *Trifolium oliganthum* Steud., *Rhus diversiloba* T. & G., *Viola howellii* Gray, *V. sempervirens* Greene, *Clarkia amoena* (Lehm.) Nels. & Macbr., *Lomatium utriculatum* (Nutt.) Coult. & Rose, *Arbutus menziesii* Pursh, *Arctostaphylos columbiana* Piper, *Vaccinium ovatum* Pursh, *Dodecatheon hendersonii* Gray, *Navarretia squarrosa* (Esch.) H. & A., *Hydrophyllum tenuipes* Heller, *Amsinckia spectabilis* F. & M., *Castilleja levisecta* Greenm., *Mimulus alsinoides* Dougl., *Orthocarpus attenuatus* Gray, *O. pusillus* Benth., *Galium cymosum* Wieg., *Plectritis congesta* (Lindl.) D.C., *Valeriana scouleri* Rydb., *Balsamorhiza deltoidea* Nutt., *Madia madioides* (Nutt.) Greene, *Microseris bigelovii* (Gray) Schultz-Bip., and *Senecio macounii* Greene.

Other vascular plants, probably of the same element, extend northward to the Puget Sound area in Washington, and occur southward to California between the coastal mountains and the Cascades. The following are representative: *Castanopsis chrysophylla* (Dougl.) D.C., *Are-*

naria paludicola Robins., *Anemone deltoidea* Hook., *Vancouveria hexandra* (Hook.) Morr. & Dec., *Lupinus albicaulis* Dougl., and *Trifolium gracilentum* T. & G.

Other elements, representing the same general distribution, extend as far north as the Columbia Gorge, thence southward into California. Still others have a restricted distribution in central Oregon: *Brodiaea hendersonii* Wats., *Pleuropogon oregonus* Chase, *Delphinium leucophaeum* Greene, *Isopyrum hallii* Gray, *Stanleya confertifolia* (Robins.) Howell, *Sidalcea campestris* Greene, *Lomatium bradshawii* (Rose) Math. & Const., and *L. hallii* (Wats.) Coult. & Rose.

Maritime

A number of species are confined to the sea-coast, mainly to sandy shores, the latter elements having been discussed by Cooper (1936):

Polypodium scouleri Hook. & Grev., *Juncus leseurii* Bol., *Agrostis longiligula* Hitchc., *A. pallens* Trin., *Calamagrostis crassiglumis* Thurb., *C. nutkaensis* (Presl) Steud., *Poa confinis* Vasey, *P. howellii* Vasey & Scribn., *P. macrantha* Vasey, *P. pachypholis* Piper, *Salix hookeriana* Barr., *Abronia latifolia* Eschsch., *A. umbellata* Lam., *Sagina crassicaulis* Wats., *Spergularia macrotheca* (Hornem.) Heynh., *Thelypodium lasiophyllum* (H. & A.) Greene, *Sedum spathulifolium* Hook., *Saxifraga marshallii* Greene, *Filipendula occidentalis* (Wats.) Howell, *Potentilla pacifica* Howell, *Sanguisorba menziesii* Rydb., *Lathyrus littoralis* (Nutt.) Endl., *Lupinus littoralis* Dougl., *Vicia gigantea* Hook., *Sidalcea hendersonii* Wats., *S. hirtipes* Hitchc., *Angelica hendersonii* Coult. & Rose, *Conioselinum pacificum* (Wats.) Coult & Rose, *Lilaeopsis occidentalis* Coult. & Rose, *Sanicula arctopoides* H. & A., *S. bipinnatifida* Dougl., *Garrya elliptica* Dougl., *Romanzoffia tracyi* Jeps., *Castilleja litoralis* Pennell, *Orthocarpus castillejoides* Benth., *Boschniackia hookeri* Walpers, *Plantago macrocarpa* C. & S., *Lasthenia minor* (D.C.) Ornduff, *Erigeron glaucus* Ker, *Ambrosia chamissonis* (Less.) Greene, *Jaumea carnosa* (Less.) Gray, and *Senecio bolanderi* Gray.

All of these species are not equally widespread, *Poa pachypholis* being restricted to the type locality. Others extend from California to Alaska: *Calamagrostis nutkatensis, Sagina crassicaulis, Pontentilla pacifica, Vicia gigantea, Conioselinum pacificum,* and *Plantago macrocarpa.* Still others extend from southern British Columbia to California: *Salix hookeriana, Abronia latifolia, Spergularia macrantha, Sidalcea hendersonii,* and *Sanicula arctopoides,* etc. A number extend from Oregon to California: *Saxifraga marshallii, Garrya elliptica, Castilleja litoralis, Erigeron glaucus,* and *Senecio bolanderi.*

Alaska and Yukon

A considerable portion of Alaska and Yukon escaped glaciation during the Pleistocene and served as a refugium for plants. Hultén (1937;

1968) and Porsild (1951; 1966) have been the principal contributors to the knowledge of this flora and Hultén (1937; 1968) in particular, has discussed history of the flora. Although many species have expanded their ranges well beyond the boundaries of Alaska and Yukon, many others continue to be restricted to areas near the refugia.

Steere has done considerable bryological field work in Alaska and has discussed this in various papers (Steere, 1938; 1958a; 1959, Schuster & Steere, 1968) and has contributed most of the information concerning Alaskan bryophyte endemics but many of his data remain unpublished. Persson (1946a; 1946b; 1947; 1949, 1952a; 1946b; 1962; 1968) has contributed richly to the knowledge of the bryoflora of the region. Although his data have yielded no new information concerning the endemics, his detailed discussions have considerably clarified the bryogeography. Other publications concerning the bryophytes of Alaska are Evans (1900; 1901; 1914), Howe (1901), Williams (1901; 1903), Cardot and Thériot (1902), Cardot (1906), Holzinger and Frye (1921), Bartram (1938), Clark and Frye (1942; 1946; 1948), Harvill (1947; 1950), Stair (1947; 1948), Thomas (1952), Sherrard (1955; 1957), Ando, Persson and Sherrard (1957), Steere and Schofield (1956), Persson and Gjaervoll (1957; 1961), Persson and Weber (1958), Schuster and Steere (1958), Iwatsuki and Sharp (1967; 1968) and Hattori and Sharp (1968). The most complete bryogeographic summaries are by Evans (1914), Persson (1949) and Steere (1953; 1965).

Among the bryophytes the *Hygrolejeunea* has closest affinities with tropical species, the *Pterigoneurum* is largely a genus of arid regions, the *Frullania* is doubtfully distinct from the widely distributed North American endemic *F. bolanderi,* and the *Trichodon,* of close affinity with a circumboreal species, is known from a single collection and is therefore not well understood. The *Oligotrichum* is clearly distinct, and is not closely related to any western North American species.

Hepatics: *Frullania chilcootensis* Steph., *Hygrolejeunea alaskana* Schuster & Steere.

Mosses: *Oligotrichum falcatum* Steere, *Trichodon borealis* Williams, and *Pterigoneurum arcticum* Steere.

Vascular Plants.

Poaceae: *Arctagrostis poaeoides* Nash, *Poa eyerdamii* Hult., *Puccinellia triflora* Swallen, *P. interior* Sorens., and *Agrophyron yukonense* Scribn. & Merr.

Cyperaceae: *Carex jacob-peteri* Hult. and *C. microchaeta* Holm.

Salicaceae: *Salix setchelliana* Ball, *S. stolonifera* Cov., *S. arctolitoralis* Hult., and *S. athabascensis* Raup.

Betulaceae: *Betula kenaica* Evans.

Polygonaceae: *Polygonum alaskanum* (Small) Wright.

Chenopodiaceae: *Atriplex drymarioides* Standl. and *A. alaskensis* Wats.

Portulacaceae: *Claytonia bostockii* Porsild and *C. scammaniana* Hult.

Caryophyllaceae: *Stellaria alaskana* Hult. and *Melandrium macrospermum* Porsild.

Ranunculaceae: *Ranunculus turneri* Greene.

Papaveraceae: *Papaver walpolei* Porsild.

Cruciferae: *Thlaspi arcticum* Porsild, *Draba exalata* Ekman, *D. maxima* Hult., *D. olgiviensis* Hult., *Smelowskia pyriformis* Drury & Rollins, *S. borealis* (Greene) Drury & Rollins, *Erysimum angustatum* Rydb., and *Braya bartlettiana* Jordal.

Saxifragaceae: *Boykinia richardsonii* (Hook.) Gray, *Saxifraga spicata* Don, and *S. reflexa* Hook.

Leguminosae: *Lupinus kuschei* Eastw., *Astragalus polaris* Benth., *A. nutzotinensis* Rousseau, *A. williamsii* Rydb., *Oxytropis kokrinensis* Porsild, *O. scammaniana* Hult., *O. huddlesonii* Porsild, *O. glaberrima* Hult., *O. kobukensis* Welsh, *O. koyukukensis* Porsild, and *O. sheldonensis* Porsild.

Umbelliferae: *Podistera yukonensis* Math. & Const.

Primulaceae: *Douglasia arctica* Hook., *D. gormani* Constance, and *Androsace alaskana* Cov. & Standl.

Gentianaceae: *Gentiana platypetala* Griseb.

Hydrophyllaceae: *Phacelia mollis* Macbr., *Romanzoffia sitchensis* Bong., and *R. unalaschensis* Cham.

Boraginaceae: *Eritrichium splendens* Kearney and *Mertensia drummondii* (Lehm.) Don.

Scrophulariaceae: *Pentstemon gormani* Greene, *Synthyris borealis* Pennell, *Castilleja unalaschcensis* (C. & S.) Malte, *C. hyetophila* Pennell, *C. chrymactis* Pennell, *C. yukonis* Pennell, *C. annua* Pennell, *C. villosissima* Penell, and *Rhinanthus arcticus* (Sterneck) Pennell.

Campanulaceae: *Campanula aurita* Greene.

Compositae: *Haplopappus macleanii* Brandegee, *Aster yukonensis* Cronq., *Erigeron purpuratus* Greene, *E. hyperboreus* Greene, *Antennaria pallida* Nels., *A. stolonifera* Porsild, *A. alborosea* Porsild & Porsild, *A. leuchippi* Porsild, *Artemisia alaskana* Rydb., *Senecio yukonensis* Porsild, *S. hyperborealis* Grumm., *S. sheldonensis* Porsild, *Saussurea angustifolia* (Willd.) D.C., and *Taraxacum carneocoloratum* Nels.

Most of the species are, predictably, of polymorphic circumpolar genera, but the presence of a species of *Boykinia* suggests that it is a Tertiary relict (Hultén, 1968). The endemics are most richly represented in alpine and subalpine habitats, but a number are maritime and others in forests, testifying to the diversity or habitats available in the Pleistocene refugia.

Aleutian Islands

Tatewaki (1963) has suggested "Hultenia" to designate the phyto-

geographic area encompassed by the Aleutian and Commander Islands. He indicates that both flora and vegetation merit the recognition of this area and gives a detailed analysis of the floristic composition and affinities. He notes a "marked difference between the (flora of) the Commander Islands and the Aleutian Islands. There is a decided floristic depression between the first and second district." The Commander Islands flora is clearly of the Eastern Asiatic floristic Region while the Aleutian Islands are of the North American floristic Region. He terms the line between these "Tatewaki's Line." This arch of islands is envisioned as a migratory route, serving as a stepping stone corridor for the expansion of Asiatic species eastward and North American species westward. Ample floristic evidence is presented to support this concept.

No bryophyte endemics have yet been reported for the area although unpublished results of Z. Iwatsuki and A. J. Sharp suggest that such species may be present.

Except for the *Polystichum* all vascular plants are derivative species of arctic and alpine areas. The *Polystichum* has its affinities with Himalayan and Chinese species. The remaining species may be relatively "young," belonging to notoriously polymorphic genera in some cases to *Taraxacum, Draba,* and *Artemisia.*

Tatewaki notes the following: *Polystichum aleuticum* Christens., *Calamagrostis bracteolata* Vassiliev, *Elymus aleuticus* Hult., *Cerastium aleuticum* Hult., *Draba aleutica* Ekman, *Artemisia aleutica* Hult., *Taraxacum chromocarpum* Hagl., *T. eyerdamii* Hagl., and *T. oncophorum* Hagl.

Although noted for the Aleutian Islands by Tatewaki, Hultén (1968) does not indicate the presence of the *Elymus* or the *Taraxacum* species. In this flora however, the following species are essentially restricted to the Aleutian Islands, although in all cases these species extend also to the Alaskan mainland as well: *Poa hispidula* Vasey, *Poa turneri* Scribn., *Salix cyclophylla* Rydb., and *Gentiana aleutica* C. & S.

The Queen Charlotte Islands

The Queen Charlotte Islands of British Columbia have served as a refugium for a number of species, both endemics and disjunct fragments of a flora of pre-glacial times. The higher elevations, at least, escaped glaciation, and the affinities of many bryophytes and vascular plants imply that they are pre-Pleistocene relicts. Calder and Taylor (1968) have thoroughly treated the vascular flora and Persson (1958), and Schofield (1962; 1965; 1966b; 1968a; 1968b) have provided preliminary notes concerning the bryophytes.

Among the bryophytes only the endemic *Acanthocladium carlottae* Schof. has been described although there remain undescribed species of *Seligeria, Brotherella, Acanthocladium,* and *Mastopoma* (?). The latter three genera suggest a montane flora of a subtropical latitude, the rela-

tionship of each of the species being largely with the Malaysian area, and suggesting great antiquity. There is a rich representation in the Islands of species showing affinities either with East Asia or Western Europe. These are discussed later under these disjunct elements.

The endemic vascular plants are confined largely to higher elevations or to habitats of lower elevations on the flanks of the mountains. The bryophyte disjuncts and endemics show a similar restriction. In all cases relationships of the undescribed taxa is with taxa of distant unglaciated areas rather than with those of adjacent glaciated areas, emphasizing that the species are probably pre-glacial relicts.

Vascular Plants: *Isopyrum savilei* Calder & Taylor, *Saxifraga taylori* Calder & Savile, *Geum schofieldii* Calder & Taylor, *Ligusticum calderi* Math. & Const., and *Senecio newcombei* Greene.

Columbia River Gorge

Piper (1906) noted that the gorge of the Columbia River and valleys of adjacent tributaries served as an area of endemism. He noted that 16 species were endemic to the gorge. Since that time many have either been found to be more widespread or have slipped into the synonymy of more widespread species. Detling (1958), in discussing the flora of the gorge noted 7 species endemic to the gorge. *Douglasia laevigata* Gray is more widespread, and thus should be excluded. Perusal of Hitchcock, *et al.* (1955–1969) indicates that 17 species are indeed endemic to the Columbia River Gorge, although a number do extend sometimes into the Wilamette Valley or into some of the tributary watercourses of the Columbia River.

Detling (1958) suggests that the gorge served as a corridor of migration for both lowland and highland species, supporting this concept by noting disjunctions of species in the gorge and in these other areas. He suggests that the lowland migrations probably occurred during the Hypsithermal and that the montane elements migrated downwards from higher elevations during the Pleistocene refrigeration. The endemics, fragments of these floras, are suggested to be relics, restricted in their range by rather narrow environmental tolerance. Unfortunately no experimental evidence is available to support or refute this hypothesis.

A single bryophyte has been noted as endemic to the Columbia River Gorge (Hermann & Lawton, 1968): *Desmatodon columbianus* Hermann & Lawt.

Vascular Plants: *Agrostis howellii* Scribn., *Calamagrostis howellii* Vasey, *Poa leibergii* Scribn., *Allium robbinsii* Henderson, *A. pleianthum* Wats., *Salix fluviatilis* Nutt., *Bolandra oregana* Wats., *Sullivantia oregana* Wats., *Astragalus diaphanus* Dougl., *Eryngium petiolatum* Hook., *Lomatium columbianum* Math. & Const., *L. laevigatum* (Nutt.) Coult. & Rose, *Cryptantha leucophaea* (Dougl.) Pays., *Pentstemon barrettae* Gray, *Erigeron howellii* Gray, *E. oreganus* Gray, and *Hieracium longiberbe* Howell.

BOREAL

The Boreal flora is composed of four elements of particular significance: circumboreal, circumboreal maritime, boreal American, and circumboreal through anthropogenic introduction. In the boreal bryoflora the North American vegetation is dominated by circumboreal species, with remarkably few endemic taxa while in the vascular flora the conspicuous elements of the vegetation are endemic to North America, thus all tree species and most shrubby species are endemic to North America (exception: *Alnus crispa*). Many circumboreal bryophytes and herbaceous vascular plants are also conspicuous elements in the Arctic flora. Many of these species extend their ranges southward in the mountains as far as Arizona, and, in some cases, into Mexico. The woody species, on the other hand, are largely supplanted southward by western North American endemics, even in the Northern Rocky Mountains.

Circumboreal

Hepatics: *Riccardia sinuata* (Dick.) Trevis., *R. pinguis* (L.) Gray, *Pellia endiviifolia* (Dicks.) Dumort., *P. neesiana* (Gottsche.) Limpr., *P. epiphylla* (L.) Lindb., *Metzgeria conjugata* Lindb., *Moerckia flotoviana* (Nees.) Schiffn., *Blasia pusilla* L., *Fossombronia dumortieri* (Hüb. & Genth.) Lindb., *Ptilidium ciliare* (L.) Hampe, *P. pulcherrimum* (Web.) Hampe, *Lepidozia reptans* (L.) Dumort., *Bazzania trilobata* (L.) Gray, *B. tricrenata* (Wg.) Trevis., *Calypogeia neesiana* (Mass. & Carest.) Müll., *C. sphagnicola* (Arn. & Perss.) Warnst. & Loeske, *C. trichomanis* (L.) Corda, *C. fissa* (L.) Raddi, *C. suecica* (Arn. & Perss.) Müll., *Cephaloziella elachista* (Jack.) Schiffn., *C. hampeana* (Nees.) Schiffn., *C. rubella* (Nees.) Douin, *Anastrophyllum michauxii* (Web.) Buch., *Barbilophozia barbata* (Schmid.) Loeske, *B. lycopodioides* (Wallr.) Loeske, *Gymnocolea inflata* (Huds.) Dumort., *Jamesoniella autumnalis* (D.C.) Steph., *Jungermannia lanceolata* Schrad., *J. pumila* With., *J. atrovirens* Dumort., *J. tristis* Nees., *J. sphaerocarpa* Hook., *Leiocolea heterocolpos* (Thed.) Buch., *L. gillmanii* (Aust.) Evans, *Lophozia excisa* (Dicks.) Dumort., *L. marchica* (Nees.) Steph., *L. incisa* (Schrad.) Dumort., *Mylia taylori* (Hook.) Gray, *M. anomala* (Hook.) Gray, *Nardia scalaris* (Schrad.) Gray, *N. geoscyphus* (DeNot.) Lindb., *Orthocaulis kunzeanus* (Hüb.) Buch., *Plectocolea obovata* (Nees.) Mitt., *P. hyalina* (Lyell) Mitt., *Sphenolobus minutus* (Crantz.) Steph., *Lophocolea heterophylla* (Schrad.) Dumort., *L. minor* Nees., *L. cuspidata* (Nees.) Limpr., *Chiloscyphus polyanthos* (L.) Corda, *Harpanthus scutatus* (Web. & Mohr.) Spr., *Geocalyx graveolens* (Schrad.) Nees., *Plagiochila asplenioides* (L.) Dumort., *Diplophyllum taxifolium* (Wahl.) Dumort., *D. albicans* (L.) Dumort., *Scapania irrigua* (Nees.) Dumort., *S. paludicola* Loeske & Müll., *S. umbrosa* (Schrad.) Dumort., *S. undulata* (L.) Dumort., *Cephalozia bicuspidata* (L.) Dumort., *C. connivens* (Dicks.) Spr., *C. catenulata* (Hüb.) Lindb., *C.*

media Lindb., *C. macounii* Aust., *Cladopodiella fluitans* (Nees.) Spr., *Odontoschisma denudatum* (Nees) Dumort., *O. elongatum* (Lindb.) Evans, *Gymnomitrion concinnatum* Corda, *Marsupella sphacelata* (Gies.) Lindb., *M. sparsifolia* (Lindb.) Dumort., *M. emarginata* (Ehrh.) Dumort., *Radula complanata* (L.) Dumort., *Porella platyphylla* (L.) Lindb., *Preissia quadrata* (Scop.) Nees., *Conocephalum conicum* (L.) Dumort., *Reboulia hemispherica* (L.) Raddi, *Riccia sorocarpa* Bisch., *R. crystallina* L., *R. fluitans* L., and *Ricciocarpus natans* (L.) Corda.

Mosses: *Sphagnum nemoreum* Scop., *S. rubellum* Wils., *S. fimbriatum* Wils., *S. fuscum* (Schimp.) Klinggr., *S. girgensohnii* Russ., *S. papillosum* Lindb., *S. squarrosum* Crome., *Andreaea rupestris* Hedw., *Fissidens adianthoides* Hedw., *F. bryoides* Hedw., *F. osmundioides* Hedw., *Trichodon cylindricus* (Hedw.) Schimp., *Ditrichum heteromallum* (Hedw.) Britt., *Distichium capillaceum* (Hedw.) B.S.G., *Blindia acuta* (Hedw.) B.S.G., *Trematodon ambiguus* (Hedw.) Hornsch., *Dicranella heteromalla* (Hedw.) Schimp., *D. rufescens* (With.) Schimp., *D. varia* (Hedw.) Schimp., *Dicranodontium denudatum* (Brid.) Britt., *Amphidium lapponicum* (Hedw.) Schimp., *Dichondontium pellucidum* (Hedw.) Schimp., *Oncophorus wahlenbergii* Brid., *Kiaeria starkei* (Web. & Mohr.) Hag., *Dicranum elongatum* Schleich., *D. fuscescens* Turn., *D. scoparium* Hedw., *Encalypta ciliata* Hedw., *E. vulgaris* Hedw., *Tortella fragilis* (Hook.) Limpr., *T. tortuosa* (Hedw.) Limpr., *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, *Barbula convoluta* Hedw., *B. unguiculata* Hedw., *Pottia heimii* (Hedw.) Fürnr., *Tortula mucronifolia* Schwaegr., *T. norvegica* (Web.) Wahlenb., *T. ruralis* (Hedw.) Gaertn., Mey., & Scherb., *Grimmia alpicola* Hedw., *G. apocarpa* Hedw., *Racomitrium aciculare* (Hedw.) Brid., *R. canescens* (Hedw.) Brid., *R. lanuginosum* (Hedw.) Brid., *Tayloria lingulata* (Dicks.) Lindb., *Tetraplodon angustatus* (Hedw.) B.S.G., *Splachnum ampullaceum* Hedw., *Tetraphis pellucida* Hedw., *Pohlia nutans* (Hedw.) Lindb., *P. wahlenbergii* (Web. & Mohr.) Andr., *Leptobryum pyriforme* (Hedw.) Wils., *Bryum pallens* Sw., *Plagiomnium affine* (Bland.) Koponen, *Mnium spinulosum* (Voit.) Schwaegr., *Aulacomnium palustre* (Hedw.) Schwaegr., *Meesea trifaria* Crum, Steere, & Anderson, *Paludella squarrosa* (Hedw.) Brid., *Catascopium nigritum* (Hedw.) Brid., *Plagiopus oederiana* (Sw.) Limpr., *Philonotis fontana* (Hedw.) Brid., *Timmia austriaca* Hedw., *Orthotrichum obtusifolium* Brid., *O. speciosum* Nees., *Ulota phyllantha* Brid., *Fontinalis antipyretica* Hedw., *Climacium dendroides* (Hedw.) Web. & Mohr., *Neckera pennata* Hedw., *Myurella julacea* (Schwaegr.) B.S.G., *Leskea polycarpa* Hedw., *Thuidium recognitum* (Hedw.) Lindb., *Abietinella abietina* (Hedw.) Fleisch., *Cratoneuron filicinum* (Hedw.) Spruce, *Campylium stellatum* (Hedw.) Jens., *Leptodictyum riparium* (Hedw.) Warnst., *Amblystegium serpens* (Hedw.) B.S.G., *Drepanocladus aduncus* (Hedw.) Warnst., *D. uncinatus* (Hedw.) Warnst., *Hygrohypnum luridum* (Hedw.) Jenn., *Calliergon cordifolium* (Hedw.) Kindb., *Scor-*

pidium scorpioides (Hedw.) Limpr., *Tomenthypnum nitens* (Hedw.) Loeske, *Brachythecium albicans* (Hedw.) B.S.G., *B. plumosum* (Hedw.) B.S.G., *Eurhynchium praelongum* (Hedw.) B.S.G., *E. pulchellum* (Hedw.) Jenn., *Pterigynandrum filiforme* Hedw., *Orthothecium chryseum* (Schwaegr.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., *Plagiothecium denticulatum* (Hedw.) B.S.G., *Pylaisiella polyantha* (Hedw.) Grout, *Hypnum callichrom* Funck., *H. revolutum* (Mitt.) Lindb., *Isopterygium pulchellum* (Hedw.) Jaeg. & Sauerb., *Ptilium crista-castrensis* (Hedw.) DeNot., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Hylocomium splendens* (Hedw.) B.S.G., *Atrichum undulatum* (Hedw.) Beauv., *Pogonatum alpinum* (Hedw.) Rohl., *P. urnigerum* (Hedw.) Beauv., and *Polytrichum piliferum* Hedw.

Vascular Plants.

Lycopodiaceae: *Lycopodium annotinum* L. and *L. clavatum* L.

Selaginellaceae: *Selaginella selaginioides* (L.) Link.

Equisetaceae: *Equisetum variegatum* Schleich., *E. fluviatile* L., and *E. arvense* L.

Ophioglossaceae: *Botrychium lunaria* (L.) Sw.

Polypodiaceae: *Pteridium aquilinum* (L.) Kuhn, *Thelypteris phegopteris* (L.) Slosson, *Athyrium filix-femina* (L.) Roth., *Cystoperis fragilis* (L.) Bernh., *Woodsia ilvensis* (L.) R.Br., *Dryopteris dilatata* (Hoffm.) Gray, and *Gymnocarpium dryopteris* (L.) Newm.

Cupressaceae: *Juniperus communis* L.

Typhaceae: *Typha latifolia* L.

Sparganiaceae: *Sparganium augustifolium* Michx.

Potamogetonaceae: *Potamogeton natans* L., *P. gramineus* L., and *P. filiformis* Pers.

Scheuchzeriaceae: *Scheuchzeria palustris* L.

Poaceae: *Phalaris arundinacea* L., *Hierochloe odorata* (L.) Wahlenb., *Alopocurus aequalis* Sobol., *Cinna latifolia* (Trev.) Griseb., *Agrostis borealis* Hartm., *Calamagrostis neglecta* (Ehrh.) Gaertn., Mey., & Scherb., *Trisetum spicatum* (L.) Richter, *Beckmannia erucaeformis* (L.) Host, *Poa glauca* Vahl, *P. palustris* L., *Glyceria maxima* (Hartm.) Holmb., and *Bromus inermis* Leyss.

Cyperaceae: *Eriophorum angustifolium* Honck., *Trichophorum caespitosum* (L.) Hartm., *Eleocharis uniglumis* (Link.) Schult., *Rhynchospora alba* (L.) Vahl., *Carex pauciflora* Lightf., *C. diandra* Schrank, *C. canescens* L., *C. disperma* Dew., *C. limosa* L., and *C. rostrata* Stokes.

Araceae: *Calla palustris* L.

Juncaceae: *Juncus alpinus* Vill., *J. articulatus L.*, and *Luzula parviflora* (Ehr.) Desv.

Orchidaceae: *Cypripedium calceolus* L., *Listera cordata* (L.) R.Br., *Platanthera obtusata* (Pursh) Lindb., *Goodyera repens* (L.) R.Br., *Corrallorhiza trifida* Chatelain, and *Calypso bulbosa* (L.) Richb. f.

Salicaceae: *Salix phylicifolia* L.

Myricaceae: *Myrica gale* L.
Betulaceae: *Betula nana* L.
Polygonaceae: *Koenigia islandica* L. and *Polygonum amphibium* L.
Caryophyllaceae: *Chenopodium glaucum* L., *Stellaria longifolia* Muhl., *S. calycantha* (Ledeb.) Bong., *Cerastium arvense* L., *Sagina nodosa* (L.) Fenzl., and *Moehringia lateriflora* (L.) Fenzl.
Ceratophyllaceae: *Ceratophyllum demersum* L.
Ranunculaceae: *Caltha palustris* L., *Ranunculus trichophyllus* Chaix., and *R. sceleratus* L.
Cruciferae: *Subularia aquatica* L., *Cardamine pratensis* L., and *Arabis hirsuta* (L.) Scop.
Droseraceae: *Drosera rotundifolia* L.
Crassulaceae: *Sedum rosea* (L.) Scop.
Rosaceae: *Rubus chamaemorus* L., *Potentilla palustris* (L.) Scop., *P. fruticosa* L., and *Sanguisorba officinalis* L.
Leguminosae: *Hedysarum alpinum* L.
Linaceae: *Linum perenne* L.
Callitrichaceae: *Callitriche hermaproditica* L.
Violaceae: *Viola selkirkii* Pursh.
Onagraceae: *Epilobium angustifolium* L., *E. palustre* L., and *Circaea alpina* L.
Haloragidaceae: *Myriophyllum verticellatum* L.
Cornaceae: *Cornus suecica* L.
Ericaceae: *Pyrola secunda* L., *Moneses uniflora* (L.) Gray, *Monotropa hypopitys* L., *Empetrum nigrum* L., *Ledum palustre* L., *Andromeda polifolia* L., *Chamaedaphne calyculata* (L.) Moench., *Arctostaphylos uva-ursi* (L.) Spreng., *Vaccinium vitis-idaea* L., *V. uliginosum* L., and *Oxycoccus microcarpus* Turcz.
Primulaceae: *Androsace septentrionalis* L., and *Lysimachia thyrsiflora* L.
Labiatae: *Scutellaria galericulata* L., *Stachys palustris* L., and *Mentha arvensis* L.
Scrophulariaceae: *Limosella aquatica* L. and *Veronica scutellata* L.
Lentibulariaceae: *Utricularia intermedia* Hayne and *U. vulgaris* L.
Rubiaceae: *Galium boreale* L. and *G. triflorum* Michx.
Caprifoliaceae: *Sambucus racemosa* L. and *Linnaea borealis* L.
Campanulaceae: *Campanula rotundifolia* L.
Compositae: *Erigeron acris* L. and *Senecio congestus* (R.Br.) D.C.

Circumboreal Maritime

No hepatics are restricted to sea-shores although several tolerate some salinity. Among the mosses only two are essentially restricted to maritime habitats, both occurring on rocks affected by salt spray: *Grimmia maritima* Turn. and *Ulota phyllantha* Brid. Other mosses are tolerant of salt spray, but are not restricted to such habitats.

Among the vascular plants are a number of obligate halophytes. In

some cases these are found away from the sea-coast, but generally in saline or alkaline environments. In North America there are some exceptions, e.g., *Lathyrus maritimus* in the Great Lakes area, *Armeria maritima* in the Rocky Mountains.

Vascular Plants: *Zostera marina* L., *Ruppia spiralis* L., *Calamagrostis deschampsioides* Trin., *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Elymus arenarius* L., *Carex glareosa* Wahlenb., *C. mackenziei* Krecz., *Stellaria humifusa* Rottb., *Honckenya peploides* (L.) Ehrh., *Cochlearia officinalis* L., *Potentilla egedii* Wormsk., *Lathyrus maritimus* L., *Hippuris tetraphylla* L. f., *Ligusticum scoticum* L., *Armeria maritima* (Mill.) Willd., *Mertensia maritima* (L.) Gray, and *Tripleurospermum phaeocephalum* (Rupr.) Pobed.

Boreal American

This element is composed of endemic species of wide distribution in northern North America. The number and vegetational importance of endemic bryophytes of this distribution pattern is not significant but the vascular plants, particularly woody species, are main components of the vegetation.

Hepatics: *Plectocolea obscura* Evans is the only species that can be placed here and even this species is uncertain, being reported from Northeastern United States and Oregon. The latter record needs verification.

Mosses: *Seligeria campylopoda* Kindb., *Grimmia dupretii* Ther., *Physcomitrium immersum* Sull., *Philonotis americana* Dism., and *Climacium americanum* Brid.

Few of these species are common, the exceptions being *Philonotis americana* and *Climacium americanum*. The others are infrequent and in rather specialized habitats.

Vascular Plants (dominant or conspicuous elements of the vegetation are designated by an asterisk).

Pinaceae: *Pinus banksiana* Lamb.,* *Larix laricina* (DuRoi) Koch.,* *Picea glauca* (Moench.) Voss.,* and *P. mariana* (Mill.) Britt., Sterns., Pogg.*

Cupressaceae: *Juniperus horizontalis* Moench.*

Sparganiaceae: *Sparganium eurycarpum* Engelm. and *S. multipedunculatum* (Morong.) Rydb.

Potamogetonaceae: *Potamogeton epihydrus* Raf. and *P. foliosus* Raf.

Alismataceae: *Sagittaria cuneata* Sheld.

Poaceae: *Oryzopsis pungens* (Torr.) Hitchc., *Muhlenbergia richardsonis* (Willd.) Trin., *M. glomerata* (Willd.) Trev., *Agrostis geminata* Trin., *Calamagrostis canadensis* (Michx.) Beauv.,* *Danthonia spicata* (L.) Beauv., *Sphenopholis intermedia* (Rydb.) Rydb., *Glyceria borealis* (Nash) Batchelder, *G. striata* (Lam.) Hitchc., *Festuca saximontana*

Rydb., *Agropyron smithii* Rydb., *A. subsecundum* (Link.) Hitchc., and *A. pauciflorum* (Schwein.) Hitchc.

Cyperaceae: *Eriophorum viridi-carinatum* (Engelm.) Fern., *Scirpus subterminalis* Torr., *S. americanus* Pers., *S. paludosus* Nels., *S. validus* Vahl.,* *S. microcarpus* Presl., *Carex leptalea* Wahlenb., *C. bebbii* Olney, *C. crawfordii* Fern., *C. aenea* Fern., *C. arcta* Boott, *C. interior* Bailey, *C. deweyana* Schwein., *C. aurea* Nutt., *C. garberi* Fern., *C. deflexa* Hornem., *C. concinna* R.Br., *C. eburnea* Brott, and *C. lanuginosa* Michx.

Juncaceae: *Juncus nodosus* L.

Liliaceae: *Smilacina racemosa* (L.) Desf. and *S. stellata* (L.) Desf.

Iridaceae: *Sisyrinchium montanum* Greene.

Orchidaceae: *Amerorchis rotundifolia* (Banks) Hult., *Platanthera orbiculata* (Pursh) Lindb., *P. dilatata* (Pursh) Lindb., *Listera convallarioides* (Sw.) Nutt., and *Corallorhiza maculata* Raf.

Salicaceae: *Populus balsamifera* L.,* *P. tremuloides* Michx.,* *Salix arctophila* Cockerell.,* *S. brachycarpa* Nutt., *S. pedicellaris* Pursh, *S. mackenzieana* Barratt, *S. myrtillifolia* Anderss., *S. candida* Flügge, and *S. interior* Rowlee.

Betulaceae: *Betula glandulosa* Michx.* and *B. papyrifera* Marsh.*

Urticaceae: *Urtica gracilis* Ait.

Santalaceae: *Geocaulon lividum* (Richards.) Fern.

Polygonaceae: *Rumex fenestratus* Greene, *Polygonum pennsylvanicum* L., and *P. achoreum* Blake.

Caryophyllaceae: *Arenaria dawsonensis* (Britt.) Mattf.

Nymphaeaceae: *Nuphar variegatum* Engelm.

Ranunculaceae: *Actaea rubra* (Ait.) Willd., *Anemone multifida* Poir., *Ranunculus abortivus* L., *R. pennsylvanicus* L. f., and, *R. macounii* Britt.

Fumariaceae: *Corydalis aurea* Willd. and *C. sempervirens* (L.) Pers.

Cruciferae: *Rorippa obtusa* (Nutt.) Britt., *Cardamine pennsylvanica* Muhl., *Draba aurea* Vahl., *Descurainia richardsonii* (Sweet) Schulz, *Arabis arenicola* (Richards.) Gelert, and *Erysimum inconspicum* (Wats.) MacM.

Saxifragaceae: *Saxifraga tricuspidata* Rottb., *Ribes oxycanthoides* L., *R. hudsonianum* Richards., and *R. glandulosum* Grauer.

Rosaceae: *Rubus pubescens* Raf., *R. arcticus* L., *Fragaria virginiana* Duchesne, *Potentilla vahliana* Lehm., *P. argentea* Pursh, and *P. pennsylvanica* L.

Leguminosae: *Oxytropis deflexa* (Pall.) D.C., *Hedysarum mackenziei* Richards. and *Vicia americana* Mühl.

Geraniaceae: *Geranium bicknellii* Britt.

Violaceae: *Viola adunca* Sm. and *V. renifolia* Gray.

Elaeagnaceae: *Shepherdia canadensis* (L.) Nutt.* and *Elaeagnus commutata* Bernh.

Onagraceae: *Epilobium leptophyllum* Raf.

Umbelliferae: *Cicuta bulbifera* L.

Ericaceae: *Ledum groenlandicum* Oeder,* *Kalmia polifolia* Wang., and *Vaccinium caespitosum* Michx.

Primulaceae: *Primula mistassinica* Michx.

Apocynaceae: *Apocynum androsaemifolium* L.

Labiatae: *Dracocephalum parviflorum* Nutt.

Scrophulariaceae: *Euphrasia disjuncta* Fern. & Wieg. and *Pedicularis groenlandica* Retz.

Rubiaceae: *Galium brandegei* Gray.

Caprifoliaceae: *Viburnum edule* (Michx.) Raf., *Symphoriocarpus albus* (L.) Blake,* and *Lonicera involucrata* (Richards.) Banks.

Compositae: *Solidago multiradiata* Ait., *S. canadensis* L., *Aster laevis* L., *A. junciformis* L., *Erigeron compositus* Pursh, *E. hyssopifolius* Michx., *E. elatus* Greene, *E. philadelphicus* L., *Antennaria pulcherrima* (Hook.) Greene, *Achillea lanulosa* Nutt., *Artemisia canadensis* Michx., *Petasites sagittatus* (Banks) Gray, *Senecio pauciflorus* Pursh, *S. pauperculus* Michx., *Taraxacum lacerum* Greene, and *Lactuca biennis* (Moench.) Fern.

Circumboreal by Anthropogenic Introduction

In the bryophytes it is rather difficult to determine anthropogenic introductions since such a high proportion of the species show a natural circumboreal distribution. Certainly the distribution of many circumboreal species have been anthropogenically expanded by destruction of competing native vascular plants and by clearing sites, but in many cases, if abandoned by man, such sites revert to a covering of vascular plant vegetation and thus bryophytes are eliminated. In cities, however, a number of presumably introduced species do persist in gardens and on stone or concrete walls, and sometimes as lawn weeds. Most of the species are also natural elements of the local flora, thus invasion of the urban sites cannot be confidently attributed to anthropogenic introduction. Among such bryophytes are:

Hepatics: *Blasia pusilla* L. and *Marchantia polymorpha* L.

Mosses: *Ceratodon purpureus* (Hedw.) Brid., *Dicranoweisia cirrata* (Hedw.) Lindb., *Barbula vinealis* Brid., *Pottia truncata* (Hedw.) Fürnr., *Tortula ruralis* Hedw., *T. muralis* Hedw., *Grimmia apocarpa* Hedw., *Funaria hygrometrica* Hedw., *Pohlia annotina* (Hedw.) Lindb., *Leptobryum pyriforme* (Hedw.) Wils., *Bryum argenteum* Hedw., *Calliergonella cuspidata* (Hedw) Loeske, *Brachythecium albicans* (Hedw.) B.S.G., *Eurhynchium praelongum* (Hedw.) B.S.G., and *Rhytidiadelphus squarrosus* (Hedw.) Warnst.

It should be noted that most of these bryophytes are common elements of the natural circumboreal flora, but their invasion of anthropogenic environments has considerably expanded their local ranges. The vascular plants, on the other hand, are mainly accidental introductions

and in many cases are noxious weeds of arable land. Many species were introduced first in eastern North America and have expanded their ranges westward with the activity of man. Many were introduced in ship's ballast, others with seeds of domestic crops and a number have escaped from cultivation.

Vascular Plants

Poaceae: *Anthoxanthum odoratum* L., *Phleum pratense* L., *Alopecurus pratensis* L., *Agrostis tenuis* Sibth., *A. stolonifera* L., *Holcus lanatus* L., *Avena fatua* L., *A. sativa* L., *Arrhenatherum elatius* (L.) Presl & Presl, *Dactylis glomerata* L., *Poa trivialis* L., *P. pratensis* L., *P. annua* L., *Festuca arundinacea* Schreb., *Bromus tectorum* L., *B. secalinus* L., *Lolium perenne* L., *L. tementulum* L., *Agropyron pecteniforme* Roem. & Schult., and *A. repens* (L.) Beauv.

Urticaceae: *Urtica urens* L.

Polygonaceae: *Rumex acetosella* L., *R. acetosa* L., *R. obtusifolius* L., *R. crispus* L., *Polygonum convolvulus* L., *P. persicaria* L., *P. hydropiper* L., and *P. aviculare* L.

Chenopodiaceae: *Chenopodium rubrum* L. and *C. album* L.

Caryophyllaceae: *Stellaria media* (L.) Vill., *Spergularia rubra* (L.) Presl & Presl, *Agrostemma githago* L., *Melandrium noctiflorum* (L.) Fries, and *Vaccaria pyramidata* Medic.

Ranunculaceae: *Ranunculus repens* L. and *R. acris* L.

Papaveraceae: *Papaver rhoeas* L.

Cruciferae: *Lepidium sativum* L., *Thlaspi arvense* L., *Sisyrinchium officinale* (L.) Scop., *S. altissimum* L., *Sinapsis arvensis* L., *Brassica juncea* (L.) Czern., *B. rapa* L., *Raphanus sativus* L., *Rorippa nasturtium-aquaticum* (L.) Hayek., *Capsella bursa-pastoris* (L.) Medic., *Neslia paniculata* (L.) Desv., *Descurainia sophia* (L.) Prantl, *Turritis glabra* L., *Erysimum cheiranthoides* L., andd *Hesperis matronalis* L.

Leguminosae: *Medicago sativa* L., *M. lupulina* L., *Melilotus officinalis* (L.) Lam., *M. albus* Desv., *Trifolium hybridum* L., *T. repens* L., *T. pratense* L., *Vicia angustifolia* (L.) Reichard., and *V. cracca* L.

Gerianaceae: *Geranium robertianum* L.

Umbelliferae: *Pastinaca sativa* L.

Boraginaceae: *Lappula myosotis* Moench. and *Myosotis palustris* L.

Labiatae: *Nepeta cataria* L., *Glechoma hederacea* L., and *Galeopsis bifida* Boenn.

Scrophulariaceae: *Linaria vulgaris* Mill., *Veronica anagallis-aquatica* L., *V. persica* Poir., and *V. arvensis* L.

Plantaginaceae: *Plantago lanceolata* L. and *P. major* L.

Compositae: *Gnaphalium uliginosum* L., *Anthemis cotula* L., *Matricaria matricarioides* (Less.) Porter, *Tripleurospermum inodorum* (L.) Schultz-Bip., *Chrysanthemum vulgare* (L.) Bernh., *Senecio vulgaris* L., *Cirsium arvense* (L.) Scop., *C. vulgare* (Savi) Ten., *Leontodon autumnalis* L., *Taraxacum officinale* Weber, and *Crepis tectorum* L.

CIRCUMARCTIC

A number of species are restricted to arctic regions, rarely extending into the subarctic. Steere (1953; 1965) has discussed the bryogeographic element and Porsild (1957) has noted vascular plants of this distributional type.

Hepatics: *Mesoptychia sahlbergii* (Lindb., & Arn.) Evans, *Lophozia latifolia* Schuster, and *Plagiochila arctica* Bryhn. & Kaalas.

Musci: *Psilopilum laevigatum* (Wahlenb.) Limpr., *Distichium hagenii* Ryan, *Blindia polaris* (Berggr.) Hag., *Haplodon wormskjoldii* (Hornem.) R.Br., *Tetraplodon paradoxus* (R.Br.) Hagen, *Pohlia crudoides* (Sull. & Lesq.) Broth., *Bryum wrightii* Sull., *Cyrtomnium hymenophyllum* (B.S.G.) Holmen, *Cinclidium latifolium* Lindb., *C. subrotundum* Lindb., and *Aulacomnium acuminatum* (Lindb. & Arn.) Par.

Vascular Plants: *Arctagrostis latifolia* (R.Br.) Griseb., *Colpodium vahlianum* (Liebm.) Nevski, *Arctophila fulva* (Trin.) Anderss., *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Agropyron boreale* (Turcz.) Drobov, *Eriophorum triste* (T. Fries) Löve & Hadac, *Carex subspathacea Wormskj., C. adelostoma* Krecz., *C. krausei* Beocl, *Luzula arctica* Blytt., *Salix arctica* Pall., *Cerastium regelii* Ostenf., *Minuartia strictat* (Sw.) Kiern., *Ranunculus confervoides* (Fries) Fries, *R. pallasii* Schlecht., *R. lapponicus* L., *R. sulphureus* Soland., *Cochlearia officinalis* L., *Eutrema edwardsii* R.Br., *Draba subcapitata* Simm., *D. micropetala* Hook., *D. alpina* L., *D. macrocarpa* Adams, *Braya purpurascens* (R.Br.) Bunge, *Saxifraga hieracifolia* Waldst. & Kit., *S. foliolosa* R.Br., *Potentilla hyparctica* Malt, *P. pulchella* R.Br., *Dryas octopetala* L., *Pyrola grandiflora* Radius, *Cassiope tetragona* (L.) Dvn., *Lomatogonium rotatum* (L.) Fries., *Pedicularis lapponica* L., and *Erigeron eriocephalus* Vahl.

ARCTIC-ALPINE

Hultén (1937) has suggested that, for species of this distributional pattern, Arctic-Montane is more appropriate, since this does not imply that the species are present in the European Alps. Although this is true, the term alpine has been used traditionally in a more general way, denoting any montane area above tree line. Arctic-alpine, as generally used, indicates that a species is widespread in Arctic regions, i.e., north of tree-line, and extends southward in higher elevations of mountains or in sites edaphically equivalent (cliffs, bogs, headlands, etc.). It has been shown (Mooney and Billings, 1961; Mooney and Johnson, 1965) that, among the flowering plants, the alpine populations of arctic alpine species represent ecotypes in those species that have been experimentally examined. It is possible that the bryophytes of this distribution also possess ecotypes. In the bryophytes, however, vegetative reproduction decreases selection and thus segregation of ecotypes is greatly impeded. Persistence of bryophytes in microenvironments that closely match the

macroenvironment of arctic regions would also work against the type of selection that leads to alpine ecotypes in vascular plants.

Hepatics: *Anthelia julacea* (L.) Dumort., *A. juratzkana* (Limpr.) Trevis, *Cephaloziella arctica* Bryhn. & Douin, *Arnellia fennica* (Gottsche.) Lindb., *Isopaches bicrenatus* (Schmid.) Buch., *Leiocolea badensis* (Gottsche.) Joerg., *L. bantriensis* (Hook.) Joerg., *L. muelleri* (Nees.) Joerg., *Lophozia longiflora* (Nees.) Schiffn., *L. ventricosa* (Dicks.) Dumort., *L. alpestris* (Schleich.) Evans, *L. wenzelii* (Nees.) Steph., *L. longidens* (Lindb.) Macoun, *Orthocaulis binsteadii* (Kaal.) Buch., *O. attenuatus* (Mart.) Evans, *O. quadrilobus* (Lindb.) Buch., *Saccobasis polita* (Nees.) Buch., *Tritomaria exsecta* (Schmid.) Schiffn., *T. exsectiformis* (Breidler) Schiffn., *T. quinquedentata* (Huds.) Buch., *Harpanthus flotowianus* Nees., *Scapania cuspiduligera* (Nees.) Müll., *S. uglinosa* (Sw.) Dumort., *S. subalpina* (Nees.) Dumort., *S. paludosa* (Müll.) Müll., *Cephalozia pleniceps* (Aust.) Lindb., *C. ambigua* Mass., *C. striatula* Jens., *Pleuroclada albescens* (Hook.) Spr.,*Gymnomitrion coralloides* Nees., *Marchantia alpestris* Nees., *Mannia pilosa* (Hornem.) Frye & Clark, *Asterella ludwigii* (Schwaegr.) Underw., *Peltolepis quadrata* (Sauter) Müll., *Clevea hyalina* (Sommerf.) Lindb., and *Sauteria alpina* Nees.

Mosses: *Trematodon brevicollis* Hornsch., *Arctoa fulvella* (Dicks.) B.S.G., *Dicranum acutifolium* (Lindb. & Arn.) Jens., *D. elongatum* Schleich., *Encalypta affinis* Hedw. f., *E. brevicolla* (B.S.G.) Bruch., *Molendoa tenuinervis* Limpr., *Barbula icmadophila* Schimp., *Didymodon rufus* Lor., *Pottia heimii* (Hedw.) Fürn., *Stegonia latifolia* (Schwaegr.) Vent., *Desmatodon systylius* B.S.G., *D. laureri* (Schulz.) B.S.G., *Voitia nivalis* Hornsch., *Tayloria froelichiana* (Hedw.) Lindb., *T. splachnoides* (Schleich.) Hook.,*Pohlia schimperi* (C.M.) Andr., *P. drummondii* (C.M.) Andr. *Plagiobryum demissum* (Hoppe & Hornsch.) Lindb., *Bryum obtusifolium* Lindb., *Mnium blyttii* B.S.G., *Cyrtomnium hymenophylloides* (Hüb.) Koponen, *Cinclidium stygium* Sw., *Aulacomnium turgidum* (Wahl.) Schwaegr., *Amblyodon dealbatus* (Hedw.) B.S.G., *Conostomum tetragonum* (Hedw.) Lindb., *Bartramia ithyphylla* Brid., *Myurella tenerrima* (Brid.) Lindb., *Drepanocladus tundrae* (H. Arnell) Loeske, *Cirriphyllum cirrosum* (Schwaegr.) Grout, *Hypnum bambergeri* Schimp., *H. vaucheri* Lesq., *H. procerrimum* Mol., and *Rhytidium rugosum* (Hedw.) Kindb.

Vascular Plants: *Huperzia selago* (L.) Bernh., *Lycopodium alpinum* L., *Woodsia alpina* (Bolton) Gray, *Hierochloe alpina* (Sw.) Roem. & Schult., *Phleum commutatum* Gandoger, *Alopecurus alpinus* Sm., *Phippsia algida* (Soland.) R.Br., *Poa alpina* L., *P. arctica* R.Br., *Eriophorum scheuchzeri* Hoppe, *Kobresia myosuroides* (Vill.) Fiori & Paol., *K. simpliciuscula* (Wahlenb.) Mack., *Carex capitata* Soland., *C. microglochin* Wahlenb., *C. bicolor* All., *C. glacialis* Mack., *C. misandra* R.Br.,

Juncus biglumis L., *Luzula confusa* Lindeb., *L. spicata* (L.) D.C. *Tofieldia pusilla* (Michx.) Pers., *Salix reticulata* L., *Oxyria digyna* (L.) Hill, *Polygonum viviparum* L., *Sagina saginoides* (L.) Karst., *Minuartia rubella* (Wahlenb.) Graebn., *Silene acaulis* L., *Melandrium apetalum* (L.) Fenzl., *Ranunculus hyperboreus* Rottb., *R. nivalis* L., *Thalictrum alpinum* L., *Cardamine bellidiflora* L., *Draba nivalis* Liljebl., *D. fladnizensis* Wulf., *Erysimum pallasii* (Pursh) Fern., *Saxifraga oppositifolia* L., *S. flagellaris* Willd., *S. nivalis* L., *S. caespitosa* L., *Parnassia palustris* L., *Sibbaldia procumbens* L., *Astragalus eucosmus* Robins., *A. alpinus* L., *Oxytropis campestris* (L.) D.C., *Epilobium latifolium* L., *E. hornemannii* Rchb., *Rhododendron lapponicum* (L.) Wahlenb., *Loiseleuria procumbens* (L.) Desv., *Phyllodoce caerulea* (L.) Bab., *Arctostaphylos alpina* (L.) Spreng., *Diapensia lapponica* L., *Pedicularis sudetica* Willd., *Pinguicula vulgaris* L., *Campanula uniflora* L., *Achillea borealis* Bong., *Arnica alpina* (L.) Olin, *Taraxacum ceratophorum* (Ledeb.) D.C., and *Crepis nana* Richards.

CIRCUMALPINE

A number of plants are predominantly alpine in distribution, and not essentially arctic, although occasionally they are found in mountainous parts of the arctic. These species occur in many mountain ranges throughout the Northern Hemisphere, sometimes extending to edaphically suitable sites associated with cliffs, canyons, and river gorges. It is possible that a number of the bryophytes may ultimately prove to be arctic-alpine in distribution, but current information would place them in the present category.

Hepatics: *Haplomitrium hookeri* (Sm.) Nees., *Jungermannia cordifolia* Hook., *Nardia compressa* (Hook.) Gray, *Tritomaria scitula* (Tayl.) Joerg., *Cephalozia leucantha* Spr., *Hygrobiella laxiflora* (Hook.) Spr., *Marsupella brevissima* (Dumort.) Grolle, and *Gymnomitrion obtusum* (Lindb.) Pears.

Mosses: *Oreas martiana* (Hoppe & Hornsch.) Brid., *Aongstroemia longipes* (Sommerf.) B.S.G., *Oligotrichum hercynicum* (Hedw.) Lam. & D.C., *Grimmia mollis* B.S.G., *Oedipodium griffithianum* (Dicks.) Schwaegr., *Hygrohypnum smithii* (Swartz.) Broth., *H. alpestre* (Hedw.) Loeske, *Calliergon stramineum* (Wahl.) Kindb., *Brachythecium turgidum* B.S.G., and *B. collinum* (Schleich.) B.S.G.

Vascular Plants: *Athyrium distentifolium* Tausch., *Cystopteris montana* (Lam.) Bernh., *Vahlodea atropurpurea* (Wahlenb.) Fries, *Lloydia serotina* (L.) Rchb., *Sagina saginoides* (L.) Karst., *Anemone narcissiflora* L., *Thalictrum alpinum* L., *Sibbaldia procumbens* L., *Myosotis alpestris* Schmidt, *Aster alpinus* L., *Senecio fuscatus* (Jord. & Fourr.) Hayek., and *S. resedifolius* Less.

Many of the bryophytes are widespread in mountainous western North America and absent from Eastern North America: *Moerckia blyttii, Nardia compressa, Hygrobiella laxiflora, Oreas martiana, Aongstroemia longipes,* etc., which is the case also for several vascular plants: *Lloydia serotina, Myosotis alpestris, Senecio fuscatus,* and *Aster alpinus.*

DISCONTINUOUS DISTRIBUTIONS

In the flora of northwestern North America there are several striking disjunct elements. For most local disjunctions the details are presently not apparent, particularly in the bryoflora. Only further collections will expose these if they do exist. For the more dramatic disjunctions, however, the evidence is clear and, in many cases, the species involved are environmentally restricted. Thus the western European disjuncts in western North America are predominantly confined to oceanic environments and are unlikely to be found across North America since the environment is unavailable there. The situation for coastal and semi-arid elements with affinities in southern South America is similar.

Western American Bicentric Alpine

A number of species, independent of their gross distributional pattern, show a disjunction within western North America suggesting that in this geographic area, at least, the Pleistocene glaciations eradicated the intervening portions of their range, leaving only those portions that survived and later expanded outward from their glacial refuges. Since suitable habitats are available in the intervening areas it must be assumed that the species are in some way prevented from merging the two western American fragments of their distribution. All species showing this pattern are alpine; they are segregated here under their general distributional element. Weber (1965) has discussed this disjunction for the Southern Rocky Mountains.

1. Arctic-alpine: *Alopecurus alpinus* Sm., *Poa vaseyochloa* Scribn., *Salix polaris* Wahlenb., *Minuartia biflora* (L.) Schinz. & Thell., *Saxifraga hirculus* L., *S. foliolosa* R.Br., and *Gentiana tenella* Rottb.

2. Endemic Western American alpine: *Poa nevadensis* Vasey, *Salix dodgeana* Rydb., *Silene douglasii* Hook., *Draba densifolia* Nutt., *Arabis lemmonii* Wats., *Potentilla virgulata* Nels., *Phlox hoodii* Richards., *Townsendia hookeri* Beaman, *Erigeron pumilus* Nutt., and *Artemisia cana* Pursh.

3. Circumarctic: *Phippsia algida* (Soland.) R.Br., *Carex rupestris* All., and *Draba fladnizensis* Wulf.

4. Circumalpine: *Swertia perennis* L.

5. Eurasia—Western American: *Silene repens* Patrin., *Anemone narcissiflora L., Viola biflora* L., and *Gentiana algida* Pall.

6. Asia—Western American: *Kobresia sibirica* Turcz., *Ranunculus gelidus* Karel & Kiril, *Smelowskia calycina* (Steph.) Mey., *Bupleurum triradiatum* Adams, and *Androsace filiformis* Retz.

Details of bryophyte distributions are presently insufficient to determine whether this distribution pattern is followed by these plants.

Affinities with Asia

This floristic element has probably received more attention than any other in the geographic region under consideration. Gray (1859) had noted the relationships in the vascular flora and these have been treated in greater detail by Hultén (1928; 1937), Hara (1939), Li (1952(, Tatewaki (1963) and briefly by Schofield (1965). The bryoflora has been considered in greatest detail by Persson (1946a; 1946b; 1947; 1052a; 1952b; 1958; 1962; 1963). Other discussions have been by Holzinger & Frye (1921), Persson and Gjaervoll (1957; 1961), Persson and Weber (1958), Steere (1959), Steere and Schofield (1956), Steere and Schuster (1960), Schofield (1965; 1966; 1968a; 1968b) and Iwatsuki and Sharp (1967; 1968). Other floristic treatments are also included in the literature cited, and it is from these that the following details have been derived.

The Asiatic affinities can be segregated into several distinct elements: Amphi–Beringian, North Pacific, East Asian–North American and Eurasian–Western American. Further subdivisions could be made, particularly in the vascular flora. In the bryoflora, however, even many of the above categories are not clearly demonstrable.

Amphi-Beringian

In this element are included species found on both sides of the Bering sea, extending into Siberia on the Asian side and into Alaska in North America. Some species found in China have also be included. In all cases the distribution appears to expand both eastward and westward from the Bering Sea area.

Hepatics: *Pseudolepicolea fryei* Perss. (Grolle & Ando), *Ascidota blepharophylla* Mass., and *Radula prolifera* Arnell.

Pseudolepicolea fryei is also found in a single locality on the west coast of Hudson Bay (Schuster, 1966).

Mosses: *Gollania turgens* (C. Müll.) Ando might be placed here, although its distribution is in mountains of Alaska and locally in China.

Vascular Plants:

Selaginellaceae: *Selaginella siberica* (Milde) Huron.

Poaceae: *Agrostis trinii* Turcz., *Calamagrostis holmii* Lange, *Koeleria asiatica* Domin., *Poa lanata* Scribn. & Merr., *P. malacantha* Kom., *P. pseudoabbreviata* Roshev., *Colpodium wrightii* Scribn. & Merr., *Puccinellia borealis* Swallen, *P. geniculata* (Turcz.) Krecz., and *Agropyron macrourum* (Turcz.) Drobov.

Cyperaceae: *Carex lugens* Holm., *C. podocarpa* Clarke, and *C. nesophila* Holm.

Juncaceae: *Luzula rufescens* Fisch. and *L. tundricola* Gorodk.

Salicaceae: *Salix phlebophylla* Anderss., *S. rotundifolia* Trautv., *S. sphenophylla* Skvortz., *S. fuscescens* Anderss., *S. ovalifolia* Trautv., *S. chamissonis* Anderss., and *S. pulchra* Cham.

Polygonaceae: *Rumex arcticus* Trautv. and *R. sibiricus* Hult.

Portulacaceae: *Claytonia tuberosa* Pall., *C. acutifolia* Pall., and *C. sarmentosa* Mey.

Caryophyllaceae: *Cerastium maximum* L., *C. jenisejense* Hult., *Minuartia arctica* (Stev.) Aschers. & Graebn., *M. yukonensis* Hult., *A. chamissonis* Maguire, *Wilhelmsia physodes* (Fisch.) McNeill, *Melandrium taylorae* (Robins.) Tolm., and *M. taimyrense* Tolm.

Ranunculaceae: *Delphinium brachycentrum* Ledeb. and *Aconitum delphinifolium* D.C.

Fumariaceae: *Corydalis pauciflora* (Steph.) Pers.

Cruciferae: *Cardamine hyperborea* Schulz, *C. microphylla* Adams, *C. purpurea* C. & S., *Draba caesia* Adams, *D. eschscholtzii* Pohle, *D. pilosa* D.C., *D. pseudopilosa* Pohle, *D. stenopetala* Trautv., *D. kamtschatica* (Ledeb.) Bush., and *D. chamissonis* Don.

Saxifragaceae: *Saxifraga eschscholtzii* Sternb., *S. serpyllifolia* Pursh, *S. exilis* Steph., *S. nudicaulis* Don., *S. davurica* Willd., *S. unalaschensis* Sternb. and *Chrysosplenium wrightii* Fr. & Sav.

Rosaceae: *Spiraea beauverdiana* Schneid. and *Potentilla elegans* C. & S.

Leguminosae: *Astragalus umbellatus* Bunge, *Oxytropis mertensiana* Turcz., and *O. arctica* R.Br.

Umbelliferae: *Cnidium ajanense* (Regel & Tiling) Drude and *C. cnidiifolium* (Turcz.) Schischk.

Primulaceae: *Primula tschuktschorum* Kjellm., *P. cuneifolia* Ledeb., *P. borealis* Duby, *Douglasia ochotensis* (Willd.) Hook., and *Dodecatheon frigidum* C. & S.

Gentianaceae: *Gentiana barbata* Froel. and *G. glauca* Pall.

Polemoniaceae: *Phlox sibirica* L., *Eritrichium aretioides* (Cham.) D.C., and *E. chamissonis* D.C.

Scrophulariaceae: *Lagotis glauca* Gaertn., *Castilleja elegans* Malte, *C. caudata* (Pennell) Rebr., and *C. hyperborea* Pennell.

Orobanchaceae: *Boschniakia rossica* (C. & S.) Fedtsch.

Plantaginaceae: *Plantago canescens* Adams.

Valerianaceae: *Valeriana capitata* Pall.

Compositae: *Artemisia globularia* Bess., *A. glomerata* Ledeb., *A. senjavinensis* Bess., *A. laciniatiformis* Kom., *A. furcata* Bieb., *Arnica lessingii* Greene, *A. frigida* Mey., *Senecio atropurpureus* (Ledeb.) Fedtsch., *Saussurea nuda* Ledeb., *S. viscida* Hult, *Taraxacum lateritium* Dahlst., and *T. kamtschaticum* Dahlst.

North Pacific

In this category are placed species that range around the North Pacific Basin. In most cases the species do not extend into continental regions. It seems likely that many of these species did not expand their range via the Bering land bridge, but by the Aleutian Chain. In other cases these species appear to be ancient relict populations of Tertiary times. Several species persist in regions where they survived the Pleistocene and preceding glaciations. In others of wider range, the species have expanded since glaciation, but from their refugia on either side of the Pacific.

Hepatics: *Takakia lepidozioides* Hatt. & Inoue, *T. ceratophylla* (Hook.) Grolle, *Herberta himalayana* (Steph.) Miller, *Ptilidium californicum* (Aust.) Underw., *Bazzania ambigua* Lindenb., *Lepidozia filamentosa* (Lehm. & Lindenb.) Gottsche, Lindenb., & Nees, *Chandonanthus hirtellus* (Web.) Mitt., *C. pusillus* Steph., *Gymnomitrion pacificum* Grolle, *Macrodiplophyllum plicatum* (Lindb.) Perss., *M. microdontum* (Mitt.) Perss., *Scapania bolanderi* Aust., *Plagiochila satoi* Hatt., *P. rhizophora* Hatt., *P. semidecurrens* Lehm. & Lindenb., *Porella vernicosa* Lindb., *Radula obtusiloba* Steph., *R. auriculata* Steph., *Cololejeunea macounii* (Spruce) Evans, and *Apotreubia nana* (Hatt. & Inoue) Hatt. & Mizut.

Mosses: *Sphagnum guwassanense* Warnst., *S. subobesum* Warnst., *Oligotrichum parallelum* (Mitt.) Kindb., *O. aligerum* Mitt., *Bartramiopsis lyellii* (James) Kindb., *Pogonatum laterale* (Brid.) Brid., *Pohlia columbica* (Kindb.) Andr., *Trachycystis flagellaris* (Sull. & Lesq.) Lindb., *Rhizomnium nudum* (Williams) Koponen, *Ulota japonica* (Sull. & Lesq.) Mitt., *U. repens* Mitt., *Climacium japonicum* Lindb., *Pleuroziopsis ruthenica* (Weinm.) Kindb., *Bryhnia hultenii* Bart., *Myuroclada maximowiczii* (Borosz.) Steere & Schof., *Campylium adscendens* (Lindb.) Perss., *Hypnum subimponens* Lesq., *H. dieckii* Ren. & Card., *Claopodium crispifolium* (Hook.) Ren. & Card., *C. pellucinerve* (Mitt.) Best., *Lescuraea julacea* Besch. & Card., *Hypopterygium fauriei* Besch., and *Habrodon leucotrichus* (Mitt.) Perss.

Vascular Plants (those marked with an * are maritime): *Mecodium wrightii* (Bosch.) Copeland, *Deschampsia beringensis* Hult., *Poa macrocalyx* Trautv. & Mey.,* *Puccinellia pumila* (Vasey) Hitchc.,* *P. hultenii* Swallen,* *P. kamtschatica* Holmb.,* *Carex macrocephala* Willd.,* *C. elusinoides* Turcz., *C. ramenskii* Kom., *C. gmelini* H. & A.,* *C. macrochaeta* Mey., *C. spectabilis* Wew., *Juncus ensifolius* Wikstr., *J. mertensianus* Bong., *Fritillaria camschatcensis* (L.) Ker.-Gawl., *Maianthemum dilatatum* (How.) Nels. & MacBr., *Streptopus streptopoides* (Ledeb.) Frye & Rigg., *Dactylorhiza aristata* (Fisch.) Soo., *Platanthera convallariifolia* (Fisch.) Lindb., *P. chorisiana* (Cham.) Rchb., *Atriplex gmelinii*

Mey.,* *Stellaria ruscifolia* Pall., *Cerastium fischerianum* Ser., *Sagina crassicaulis* Wats.,* *Minuartia macrocarpa* (Pursh) Ostenf., *Aconitum maximum* Pall., *Ranunculus eschscholtzii* Schlecht., *Oxygraphis glacialis* (Fisch.) Bunge, *Papaver alboroseum* Hult., *Cardamine umbellata* Greene, *Draba borealis* D.C., *D. hyperborea* (L.) Desv., *Saxifraga bronchialis* L., *S. bracteata* Don, *Rubus pedatus* Sm., *R. spectabilis* Pursh, *Geum calthifolium* Menzies, *G. rossii* (R.Br.) Ser., *G. pentapetalum* (L.) Makino, *Sanguisorba stipulata* Raf., *Geranium erianthum* D.C., *Viola langsdorfii* Fisch., *Epilobium behringianum* Haussk., *E. sertulatum* Haussk., *Angelica genuflexa* Nutt., *Rhododendron camtschaticum* Pall., *Phyllodoce aleutica* (Spreng.) Heller, *Cassiope stelleriana* (Pall.) D.C., *C. lycopodioides* (Pall.) Don, *Fauria crista-galli* (Menzies) Makino, *Plagiobothrys orientalis* (L.) Johnston, *Pentstemon fruticosus* (Pursh) Greene, *Veronica stelleri* Pall., *Euphrasia mollis* (Ledeb.) Wettst., *Pedicularis chamissonis* Stev., *Pinguicula macroceras* Link., and *Hieracium triste* Willd.

A number of vascular plant genera are present only in East Asia and Western North Amreica, but are represented by different species in each of the areas: *Pseudotsuga, Phyllospadix, Lysichiton, Castanopsis, Achlys,* and *Echinopanax.*

East Asia–North American

A number of species of vascular plants are widespread in North Amerıct, particularly in boreal and arctic regions and extend into the eastern portion of Asia, occasionally westward nearly to Europe. The only bryophyte of comparable range appears to be the moss *Hypnum plicatulum* (Lindb.) Jaeg. & Sauerb.

Vascular Plants: *Lycopodium obscurum* L., *Hierochloe pauciflora* R.B., *Calamagrostis purpurascens* R.Br., *Danthonia intermedia* Vasey, *Schizachne purpurascens* (Torr.) Swallen, *Bromus ciliatus* L.,*Elymus mollis* Trin., *Eriophorum callitrix* Cham., *Carex stipata* Muhl., *C. viridula* Michx., *C. membranacea* Hook., *Smilacina trifolia* (L.) Desf., *Salix fuscescens* Anderss., *S. alaxensis* (Anderss.) Cov., *S. depressa* L., *Alnus crispa* (Ait.) Pursh, *Stellaria longipes* Goldie, *S. edwardsii* R.Br., *Cerastium beeringianum* C. & S., *Brasenia schreberi* Gmel., *Caltha natans,* Pall., *Coptis trifolia* (L.) Salisb., *Anemone richardsonii* Hook., *A. parviflora* Michx., *Rorippa hispida* (Desv.) Britt., *Lesquerella arctica* (Wormsk.) Wats., *Arabis lyrata* L., *A. drummondii* Gray, *A. divaricarpa* Nels., *A. holboellii* Hornem., *Mitella nuda* L., *Parnassia kotzebuei* C. & S., *Ribes lacustre* (Pers.) Poir., *R. triste* Pall., *Geum macrophyllum* Willd., *Oxytropis nigrescens* (Pall.) Fisch., *Sium suave* Walt., *Conioselinum chinense* (L.) B.S.G., *Angelica lucida* L., *Heracleum lanatum* Michx., *Cornus canadensis* L., *Pyrola asarifolia* Michx., *Monotropa uniflora* L., *Arctostaphylos rubra* (Rehd. & Wilson) Fern., *Lycopus lucidus* Turcz., *L. uniflorus* Michx., *Veronica americana* Schwein., *Pedicularis labradorica* Wirsing., *P. langsdorfii* Fisch., *P. capitata* Adams., *Galium kamtchaticum*

Steller., *Antennaria friesiana* (Trautv.) Ekman, *Anaphalis margaritacea* (L.) B. & H., *Artemisia frigida* Willd., *Petasites palmatus* (Ait.) Gray, *Senecio resedifolius* Less., and *S. pseudo-arnica* Less.

Eurasia–Western America

A number of species are widespread through both Asia and Europe, either in the arctic or in boreal regions, sometimes both, and extend into western North America. In most cases these plants do not extend east of the Rocky Mountains, but in some cases reach the west coast of Hudson Bay or the Great Lakes region. These are represented by only vascular plants.

Cryptogramma crispa (L.) R.Br., *Thelypteris limbosperma* (All.) Fuchs., *Ruppia spiralis* L., *Agrostis clavata* Trin., *Scolochloa festucacea* (Willd.) Link., *Carex obtusata* Lilj., *C. pyrenaica* Wahlenb., *C. lapponica* Lang., *C. rhynchophysa* Mey., *Cypripedium guttatum* Sw., *Hammarbya paludosa* (L.) Ktze., *Salix hastata* L., *Rumex graminifolius* Lamb, *Silene repens* Patrin, *Anemone narcissiflora* L., *Pulsatilla patens* (L.) Mill., *Thalictrum minus* L., *Aruncus sylvester* Kostel, *Hedysarum hedysaroides* (L.) Schinz & Thell., *Impatiens noli-tangere* L., *Viola biflora* L., *V. epipsila* Ledeb., *Ligusticum mutellinoides* (Crantz.) Willar, *Primula sibirica* Jacq., *Androsace chamaejasme* Host, *A. filiformis* Retz., *Trientalis europaea* L., *Gentiana algida* Pall., *G. prostrata* Haenke, *Swertia perennis* L., *Polemonium acutiflorum* Willd., *P. boreale* Adams, *Myosotis alpestris* Schmidt, *Pedicularis verticellata* L., *P. oederi* Vahl, *Aster alpinus* L., *A. sibiricus* L., *Artemisia laciniata* Willd., *Petasites frigidus* (L.) Franck., and *Senecio fuscatus* (Jord. & Fourr.) Hayek.

Western North America—Southern Hemisphere Disjunctions

In the western North American flora two different discontinuities are exhibited by species that reappear in the Southern Hemisphere: bi-polar disjuncts and Pacific North American–South American disjuncts.

Bipolar Disjuncts

Du-Rietz (1940) has thoroughly discussed the problem of bipolar plant distribution, summarizing both pertinent literature and basic information. A bipolar disjunct pattern is that in which species occur in the temperate Northern Hemisphere, and again in the temperate Southern Hemisphere but are essentially absent from tropical latitudes.

To explain this pattern DuRietz (1940) concluded that "it seems necessary to look for epeirogenetic transtropical highland bridges older than the mountain-chains of the Alpine Orogen. Such highland bridges may have existed not only in Africa, but also bordering the transtropical Alpine geosynclines (i.e. the Andean and the Malaysian geosynclines), partly passing over present deep sea bottom."

In many cases the plants of this disjunction are circumboreal in the Northern Hemisphere, several being ubiquitous through that range.

Sainsbury (1952) briefly discussed some of the mosses of New Zealand that showed this distributional pattern. The discussions of Martin (1946; 1949; 1952a; 1952b) have also contributed to the understanding of this disjunction.

Hepatics: *Fossombronia pusilla* (L.) Dum., *Metzgeria furcata* (L.) Dum., *Moerckia blyttii* (Moerch.) Brockm., *Anthelia juratzkana* (Limpr.) Trevis, *Ptilidium ciliare* (L.) Hampe., *Barbilophozia hatcheri* (Evans) Loeske, *Jungermannia cordifolia* Hook., *Orthocaulis floerkei* (Web. & Mohr.) Buch., and *Diplophyllum obtusifolium* (Hook.) Dumort.

Mosses: *Sphagnum centrale* C. Jens., *S. fimbriatum* Wils., *S. magellanicum* Brid., *S. palustre* L., *S. papillosum* Lindb., *S. subnitens* Russow & Warnst., *Andreaea rupestris* Hedw., *Tetrodontium brownianum* (Dicks.) Schwaegr., *Pogonatum alpinum* (Hedw.) Röhl., *Polytrichum formosum* Hedw., *Buxbaumia aphylla* Hedw., *Fissidens adianthoides* Hedw.,*Ditrichum flexicaule* (Schwaegr.) Hampe, *Saelania glaucescens* (Hedw.) Broth., *Dicranum scoparium* Hedw., *Pottia heimii* (Hedw.) Fürnr., *Desmatodon convolutus* (Brid.) Grout, *Tortula muralis* Hedw., *T. papillosa* Wils., *T. laevipila* (Brid.) Schwaegr., *Encalypta vulgaris* Hedw., *Grimmia donniana* Sm., *G. trichophylla* Grev., *Racomitrium lanuginosum* (Hedw.) Brid., *Funaria microstoma* B.S.G., *Tetraplodon mnioides* (Hedw.) B.S.G., *Bryum angustirete* Kindb., *B. pseudotriquetrum* (Hedw.) Gaertn., Mey. & Scherb., *B. caespiticium* Hedk., *B. microerythrocarpum* C. Müll. & Kindb., *Aulacomnium palustre* (Hedw.) Schwaegr., *Bartramia halleriana* Hedw., *B. pomiformis* Hedw., *B. ithyphylla* Brid., *Orthotrichum alpestre* Hornsch., *Climacium dendroides* (Hedw.) Web. & Mohr., *Neckera pennata* Hedw., *Campylium polygamum* (B.S.G.) Jens., *Leptodictyon riparium* (Hedw.) Warnst., *Drepanocladus uncinatus* (Hedw.) Warnst., *Calliergon cordifolium* (Hedw.) Kindb., *C. sarmentosum* (Wahlenb.) Kindb., *Calliergonella cuspidata* (Ren.) Grout, *Brachythecium albicans* (Hedw.) B.S.G., *B. plumosum* (Hedw.) B.S.G., *B. rutabulum* (Hedw.) B.S.G., *B. salebrosum* (Web. & Mohr) B.S.G., *B. velutinum* (Hedw.) B.S.G., *Eurhynchium praelongum* (Hedw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., *Plagiothecium denticulatum* (Hedw.) B.S.G., *P. roeseanum* B.S.G., *Hypnum revolutum* (Mitt.) Lindb.,*Isopterygium pulchellum* (Hedw.) Jaeg. & Sauerb., and *Hylocomium splendens* (Hedw.) B.S.G.

Vascular Plants:*Botrychium lunaria* (L.) Sw., *Pteridium aquilinum* (L.) Kuhn., *Asplenium trichomanes* L., *Potamogeton filiformis* Pers., *P. praelongus* Wulf., *P. natans* L., *Triglochin palustris* L., *Vahlodea atropurpurea* (Wahl.) Fries., *Carex buxbaumii* Wahl., *C. capitata* Soland., *C. canescens* L., *C. diandra* Schrank, *C. lachenalii* Schkuhr., *C. magellanica* Lam., *C. microglochin* Wahl., *C. pyrenaica* Wahl., *Juncus filiformis* L., *Koenigia islandica* L., *Chenopodium glaucum* L., *Montia fontana* L.,

Honkenia peploides (L.) Ehrh., *Anemone multifida* Poir, *Cochlearia officinalis* L., *Gentiana prostrata* Kaenke, and *Hieracium gracile* Hook.

Pacific North American—South American Disjuncts

In arid and coastal areas of Pacific North America are a number of species that reappear again in South America in Argentina and Chile, generally as elements of the same environment. These species have attracted the attention of a number of botanists: Gray and Hooker (1880), Bray (1898; 1900), Campbell (1944), Campbell and Wiggins (1947), Raven and Lewis (1959), and Cruden (1966). In a symposium concerning this disjunction, Raven (1963) provided the summary. In the same publication were detailed studies of particular species by Chambers (1963), Constance (1963), Heckard (1963), and Ornduff (1963).

No information concerning bryophytes was included and the details concerning the bryoflora are inadequate to make any valid generalizations.

Raven (1963) suggests the following theory to explain this disjunction: "The great majority of the plants reached their disjunct areas by long-distance dispersal relatively recently. For the bipolar species, the Pleistocene seems the most likely time of dispersal, for the temperate species, the late Pliocene or Pleistocene, and for the desert species, excluding those that have differentiated from common ancestors that spanned the tropics, no time has probably been more likely than the recent past. Both bipolar and temperate disjuncts have come mostly from the north and are almost entirely herbaceous. The desert disjuncts, on the other hand, often appear to have originated in the south, or have diverged from a common tropical ancestor. Many of them are woody."

As was noted earlier, DuRietz (1940) did not hold this opinion. Cruden (1966) also suggests another alternative, noting that for the examples given by Raven, birds could not have served as the dispersal agents and no other agency is likely for such great distances. He suggests that birds, other than shorebirds, may have been important in stepwise dispersal of the species for relatively short distances. "Mountain hopping provides a reasonable explanation for the movement of a large segment of the parental gene pool across the tropics through the buildup of large intermediate populations."

Unfortunately such mountains have not been available during the time suggested and one would be forced to imply a change in the ecology of the species during "migration" and reversion to the original ecological requirements on "arrival."

Species exhibiting this disjunction are (those marked * are essentially maritime): *Palleae atropurpurea* (L.) Link, *Lilaea scilloides* (Poir.) Haum., *Triglochin concinna* Burtt—Davy,* *Agrostis idahoensis,* Nash, *Bromus trinii* Desv., *Danthonia californica* Boland., *Deschampsia danthonioides* (Trin.) Munro, *D. elongata* (Hook.) Munro, *Festuca megalura* Nutt., *Poa stenantha* Trin., *P. secunda* Pres, *Carex*

praegracilis Boott, *Scirpus cernuus* Vahl.,* *S. nevadensis* Pers., *Juncus leseurii* Boland,* *Calandrinia ciliata* (R. & P.) D.C., *Oxytheca dendroidea* Nutt., *Polygonum punctatum* Ell., *Cardionema ramosissima* (Weinm.) Nels. & Macbr.,* *Anemone multifida* Poir., *Myosurus apetalus* Gay, *Lepidium nitidum* Nutt., *Fragaria chiloensis* (L.) Duch.,* *Trifolium macraei* H. & A., T. *microdon* H. & A., *Boisduvalia glabella* (Nutt.) Walpers, *Gayophytum humile* Juss., *G. diffusum* T. & G., *Osmorhiza chilensis* H. & A., *O. depauperata* Phil., *Sanicula crassicaulis* Poepp., *S. graveolens* Poepp., *Microsteris gracilis* (Hook.) Greene, *Polemonium micranthum* Benth., *Coldenia nuttallii* Hook., *Cryptantha circumscissa* (H. & A.) Johnst., *Heliotropium curassavicum* L., *Lappula redowskii* (Hornem.) Greenm., *Plectocarya linearis* (R. & P.) D.C., *Plagiobothrys scouleri* (H. & A.) Johnst., *Veronica peregrina* L., *Plantago patagonica* Jacq., *Convolvulus soldanella* L.,* *Ambrosia chamissonis* (Less.) Greene,* *Madia gracilis* (Sm.) Keck., *M. sativa* Mol., and *Psilocarphus brevissimus* Nutt.

Western North America—Western Europe

Most of the species of this element are oceanic in their distribution although a number are alpine. In both cases they appear to be persistent remnants of a circumboreal flora, possibly dating back as early as Tertiary time. To imply long-distance dispersal from Europe is illogical since suitable habitats for the species also exist in eastern North America, but the species do not occur there. Evans (1900), and Persson (1949) have discussed this element in the hepatics in particular, and Schofield (1965; 1968a; 1968b) has considered all bryophytes. The vascular flora of this disjunction was briefly discussed by Schofield (1965). Several of the species are widespread and abundant in both parts of their range, others are highly restricted.

Hepatics: *Herberta straminea* (Dumort.) Trevis, *Mastigophora woodsii* (Hook.) Nees., *Bazzania pearsonii* Steph., *Cephaloziella phyllacantha* (Mass. & Carest.) Müll., *C. turneri* (Hook.) Müull., *Anastrepta orcadensis* (Hook.) Schiffn., *Anastrophyllum donianum* (Hook.) Spr., *A. assimile* (Mitt.) Steph., *Gymnocolea acutiloba* (Kaal.) Müll., *Jungermannia caespiticia* Lindenb., *Plagiochila major* (Nees.) Arnell, *Diplophyllum obtusifolium* (Hook.) Dum., *Scapania scandica* (Arn. & Bach.) MacVicar, *Marsupella alpina* (Gottsche.) *Bernet., M. brevissima* (Dumort.) Grolle, *M. commutata* (Dumort.) Grolle, *Pleurozia purpurea* (Lightf.) Lindb., *Porella cordaeana* (Hueb.) Evans., *Metzgeria fruticulosa* (Dicks.) Evans., *Moerckia blyttii* (Moerch.) Brockm., and *Bucegia romanica* Radian.

Among the hepatics, and several of the mosses, a number of species are found in scattered localities in mountainous Japan and in the Himalayas.

Mosses: *Andreaea nivalis* Hook., *Ditrichum zonatum* (Brid.) Kindb., *Cynodontium jenneri* (Schimp.) Stirt., *Kiaeria falcata* (Hedw.) Hag., *Dicranum tauricum* Sapeh., *D. spadiceum* Zett., *Dicranodontium uncinatum* (Harv.) Jaeg., *Campylopus schwarzii* Schimp., *C. schimperi* Milde, *C. subulatus* Milde, *Paraleucobryum enerve* (Thed.) Loeske, *Encalypta affinis* Hedw., f., *E. longicollis* Bruch., *Leptodontium recurvifolium* (Tayl.) Lindb., *Barbula vinealis* Brid., *Geheebia gigantea* (Funck.) Boul., *Pottia lanceolata* (Hedw.) Müll., *Tortula subulata* Hedw., *T. laevipila* (Brid.) Schwaegr., *T. latifolia* (Spreng.) Hartm., *T. princeps* DeNot., *Grimmia pulvinata* (Hedw.) Sm., *G. decipiens* (Schultz.) Lindb., *G. hartmannii* Schimp., *Micromitrium tenerum* (B.S. G.) Crosby, *Funaria muhlenbergii* Hedw. f., *Tayloria hornschuchiana* (Gre. & Arn.) Lindb., *T. froelichiana* (Hedw.) Mitt., *Pohlia erecta* Lindb., *P. vexans* (Limpr.) Lindb. f., *P. gracilis* (B.S.G.) Lindb., *Epipterygium tozeri* (Grev.) Lindb., *Bryum miniatum* Lesq., *B. canariense* Brid., *Bartramia halleriana* Hedw., *Zygodon rupestris* (C. Hartm.) Milde, *Z. gracilis* Wils., *Orthotrichum rupestre* Schleich., *O. laevigatum* Zett., *O. speciosum* Nees., *O. rivulare* Turn., *O. cupulatum* Brid., *O. alpestre* Hornsch., *O. tenellum* Bruch., *O. pulchellum* Brunt., *Antitrichia curtipendula* (Hedw.) Brid., *Pterogonium gracile* (Hedw.) Sm., *Neckera menziesii* Hook., *Hookeria lucens* (Hedw.) Sm., *Fabronia pusilla* Raddi, *Lescuraea stenophylla* (Ren. & Card.) Kindb., *Drepanocladus trichophyllus* (Warnst.) Podp., *Hygrohypnum molle* (Hedw.) Loeske, *Calliergon megalophyllum* Mik., *Brachythecium trachypodium* (Funch) B. & S., *B. tromsoense* (Kaur. & Arn.) Limpr., *Scleropodium caespitans* (Müll.) L. Koch., *S. tourettei* (Brid.) Koch., *Plagiothecium piliferum* (Sw.) B.S.G., *P. platyphyllum* Mönk., and *P. undulatum* (Hedw.) B.S.G.

Vascular Plants: *Equisetum telmateia* Ehrh., *Blechnum spicant* (L.) Roth, *Thelypteris oreopteris* (Ehrh.) Slosson, *Carex stenophylla* Wahlenb., *C. foetida* All., and *Saxifraga adscendens* L., also the vicariant species (the European in parentheses): *Anemone drummondii* Wats. (*A. baldensis* L.), *Pulsatilla occidentalis* (Wils.) Freyn. (*A. alpinus* (L.) Debartre), *Trifolium nanum* Torr. (*T. alpinum* L.), and *Astragalus goniatus* Nutt. (*A. danicus* Retz.).

Cordilleran Disjuncts in Eastern America

Fernald (1924; 1925), in his discussion of vascular plant distribution in northeastern North America, noted a conspicuous element of western North American affinity. Many of these species are North American endemics, while others show a broken circumboreal distribution, or in some cases, affinities with Asia. In all of these, however, there is a marked disjunction between northeastern North America and Western North America. In many the western North American portion of the distribution does not extend beyond the Rocky Mountain chain.

Since the publication of the earlier papers, Fernald (1926; 1933); 1935; 1942) published the results of his considerable field-work further emphasizing this element. His explorations concentrated on areas in eastern North America that had previously yielded disjuncts and in which he located further taxa of this distribution pattern. These regions included Newfoundland, Gaspé and the shores of Lake Superior. Most frequently these plants occur in river canyons or at high elevations. Thus, many of the species appear to be part of a broken circumalpine or circumboreal distribution, or are species endemic to mountains of North America. The contributions of Marie-Victorin (1935; 1938), in his explorations of the islands of the St. Lawrence River, Anticosti and Mingan Islands, contributed further information concerning this disjunction. Abbe (1936) briefly discussed cordilleran disjuncts in Labrador peninsula, noting that they are few in number and that in many the ranges are not as interrupted as was previously assumed.

Further discussions of this element are those of Stebbins (1935), Wynne-Edwards (1937; 1939), Griggs (1940), Raymond (1950), Scoggan (1950), Böcher (1951), Butters & Abbe (1953), Rousseau (1953), Rune (1953; 1954), Dutilly, Lepage and Duman (1958), Schuster (1958), and Schofield (1959). The check-list of Newfoundland vascular plants of Rouleau (1956) is also a valuable source of basic information, as is that of Porsild and Cody (1968) for Mackenzie District.

Explanations for this disjunction are rather varied. The basic problems have been threefold: the inadequacy of details of glaciation in the pertinent areas in eastern America, the ecology of the disjuncts in their eastern outposts, and the uncertainties concerning the total ranges of the species due to inadequate collections from intervening areas. Changes in the status of these avenues of information have led to changes in the theory explaining the plant disjunctions.

Fernald (1925) felt that "Cordilleran" and particularly arctic-alpine species in eastern North America had survived on nunataks during the Pleistocene glaciations. The nunataks he considered to be essentially coincident with the areas rich in these disjunct plants. Arguments against this hypothesis have been strongest and most convincing concerning the arctic-alpine elements. Wynne-Edwards (1937; 1939), Rousseau (1950) and Dammann (1965) have noted that these species could certainly have immigrated into their present sites following glaciation and now persist in only those microclimatic sites that are not invaded by the general flora that is more adapted to the macroclimate.

Stebbins (1935) suggested that each disjunct "migrated eastward in post-glacial times, following near the front of the retreating ice-sheet. Widespread, though local, in its western distribution, it becomes rarer and rarer eastward, with a more limited range north and south, until at its eastern limit there are (few) widely separated stations for it."

Abbe (1936) to explain the presence of this element in Labrador,

where the cordilleran taxa are largely now near sea-level suggested: "Possibly then, the balance of all factors were such that in areas, as at the heads of fiords, protected from wind, warmed by occasional föhn winds and by the action of direct insolation, and with melt-water available from the ice-fields above, plants may have survived through the peak of Wisconsin glaciation in the lee of the Torngat Mountains in northeastern Labrador."

Wynne-Edwards (1937) suggested what is termed by Victorin (1938) the "rainbow hypothesis": "Some of these plants have wide limits of climatic tolerance, occurring through a wide latitudinal range, in which case their American distribution takes the form of an arch spanning the continent from the Cordillera to the St. Lawrence by way of the Arctic, while others are more confined, the hardiest occupying the crown of the arch and least hardy its two ends, whereby their ranges are disrupted into western and eastern centres."

Griggs (1940), to explain the distribution of rare plants, suggested that, for disjuncts: "rare plants have been eliminated from the older adjacent barren areas by competition with the more competent common vegetation but persist in the refuges more recently opened to colonization because the ecological succession there has not run quite so far as elsewhere." This would assume a continuity in the past distribution of the disjunct species.

Rousseau (1950) summarizes his explanation as follows: "(a) some (of the Cordilleran disjuncts) . . . could be indifferent arctic alpine plants, now absent from the Arctic proper through elimination by various historical factors (b) The remaining species after this elimination could be considered, at least hypothetically, as pre-glacial plants, though this is not the only probable explanation (c) The remaining species could, as well, be considered as simply alpine species, living on alpine formations constituted after the recess of the glacier. The plants could have taken shelter there during the "pre-sylvatic period," after having travelled from the Canadian Rockies to the Gaspé Peninsula, along the "Arctic Corridor" bordering the receding continental glacier. During glaciation these plants in the Rockies could have sought refuge either south of the glacier or on nunataks. The relicts would then be preglacial in the Rockies and postglacial in Gaspé."

Gaspé has been explored bryologically by both F. Leblanc and J. Kucyniak but the results have not yet been published. From the extensive bryological collections made in Newfoundland, Tuomikoski has published results only on the hepatics (Buch & Tuomikoski, 1955). In this paper he notes only two "Cordilleran" hepatics: *Frullania bolanderi* Aust. and *Cephalozia catenulata* (Hueb.) Spruce. He notes, however, that a number of species show this disjunct pattern in North America although they belong to the circumboreal element. These species are widely distributed through eastern North American, extend westwards

frequently to the Great Lakes and southward in the Appalachian Mountains, but are absent until west of the Rocky Mountains in many cases. They are therefore excluded here as "Cordilleran disjuncts" largely because they represent a different distributional pattern to those discussed arlier.

Steere (1937; 1938) drew attention to the bryophytes to Cordilleran disjunction in the Great Lakes areas. Schuster (1958) provided further information for this region.

Of the hepatics cited by Steere (1937; 1938), Schuster (1958) suggested that they could not be considered Cordilleran but were of much wider distribution, being found in intervening areas. He suggested that those that have not been collected in intervening areas are largely inconspicuous and will undoubtedly be found with further exploration.

It seems possible that the mosses may be similarly distributed, but the presently known ranges would support Steere's contention that they are Cordilleran disjuncts: *Racomitrium patens* (Hedw.) Hübn., *Grimmia hartmannii* Schimp., *Lescuraea incurvata* (Hedw.) Lawt., and *Hygrohypnum molle* (Schimp.) Loeske. It should be noted that these mosses are essentially circumboreal in their world-wide distribution.

The Cordilleran disjunct vascular plants can be divided into three categories (those marked with an asterisk are maritime).

1. Endemic to North America: *Cheilanthes siliquosa* Maxon, *Woodsia oregana* Eat., *Polystichum scopulinum* (Eat.) Maxon, *Poa canbyi* (Scribn.) Piper, *Festuca scabrella* Torr., *Agropyron violaceum* (Hornem.) Lange, *Eleocharis nitida* Fern., *Carex filifolia* Nutt., *Goodyera oblongifolia* Raf., *Platanthera unalaschensis* (Spreng.) Kurtz., *Salix vestita* Pursh, *Polygonum fowleri* Robins.,* *Salicornia virginica* L.,* *Minuartia obtusiloba* (Rydb.) House, *Spergularia canadensis* (Pers.) Don,* *Dryas drummondii* Richards., *Vaccinium ovalifolium* Sm., *Campanula latisepala* Hult., and *Arnica cordifolia* Hook., *A. mollis* Hook., and *Cirsium foliosum* (Hook.) D.C.

2. East Asian—western American—Eastern American disjunct: *Potamogeton subsibiricus* Hagstr., *Poa eminens* Presl,* *Eleocharis kamtschatica* (Mey.) Kom.,* *Carex lyngbaei* Hornem.,* *C. stylosa* Mey., *C. franklinii* Boott, *Juncus ensifolius* Wikstr., *Epilobium glandulosum* Lehm., *Conioselinum chinense* (L.) B.S.P., *Angelica lucida* L., *Galium kamtschaticum* Steller, *Arnica frigida* Mey., *Senecio resedifolius* Less., and *S. pseudo-arnica* Less.

3. Essentially circumboreal, but in North America with western North America and eastern America disjunction: *Lycopodium inundatum* L., *Athyrium distentifolium* Tausch., *Cystopteris montana* (Lam.) Bernh., *Polystichum lonchitis* (L.) Roth., *P. braunii* (Spenn.) Fee., *Trichophorum pumilum* (Vahl.) Schinz. & Thell., *Thalictrum alpinum* L., *Ligusticum scothicum* L., and *Cornus suecica* L.

In summary, there is a marked disjunct Cordilleran element in the

flora of eastern North America, centered largely around the Gulf of St. Lawrence region and the Great Lakes. The species are largely alpine in distribution and ecology although several are maritime. In most cases they are restricted to sites relatively free from invasion by the species that dominate the general local vegetation, and are essentially in sites at a persistent pioneering phase.

The most plausible explanation of their disjunction is that the eastern representatives are remnants of a more widespread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America. The Pleistocene glaciations can be assumed to have eliminated the north-central portion of the range, but since habitats were available in north-eastern and western North America the species survived, probably south of the glacial boundary, but possibly in nunataks or coastal refuges, moving to their present sites following retreat of the ice sheet but being eliminated from their Pleistocene refugium by the encroaching vegetation and by a succession toward more mesophytic temperate vegetation. Evidence for nunataks and refugia in eastern North America has been disputed.

SUMMARY

The flora of northwestern North America is composed of a rich representation of endemics, both in genera and species. Highest concentration of these is in areas that are environmentally diverse and escaped the Pleistocene glaciations. Although the glaciated areas also possess many endemics, their flora tends to be dominated by circumboreal taxa, greatest in Alaska and northern British Columbia, and decreasing southward.

That much of the western North American flora is a fragment of a more widespread flora of Eurasian affinities appears indisputable. Why, in many cases, these taxa have not extended their range across North America, or remain as persistent remnants in suitable environments on both sides of the continents, can probably never be adequately explained. Reconstruction of the climatic and accompanying geologic events as reflected by the records of past floras will considerably aid in the proposition of a working hypothesis. However, new information will always make necessary modification of the historical details that have led to present distributions.

In vascular plants, in particular, the ranges of taxa have been greatly altered by man's activities. The introduction of exotic species of vascular plants has also greatly affected the species that formed the native flora that preceded the advent of man. The effects of aboriginal man on plant introductions have never been adequately studied.

In bryophytes such introductions are presumed to be relatively infrequent but man's influence on distribution patterns has been drastic in environments that are readily exploited by man. Since bryophytes are frequently found in rather extreme environments and persist in small microclimatic sites, they may remain while the more vulnerable

vascular flora succumbs. Thus the bryophytes serve as a valuable tool to interpret past floristic history. From the hypotheses derived from bryophyte distributions one can extrapolate to vascular plant distributions.

The bryoflora of western North America consists of a considerably higher percentage of elements of circumboreal distribution than does the vascular flora. The presence of remarkably wide disjuncts is also generally more conspicuous in the bryophytes than in the vascular flora. This is emphasized by disjunction of species of western Europe—western North America and also of a number of species of southeast Asia—western North America. Especially notable about these taxa is the fact that most lack sexual reproduction and have no special means of asexual reproduction. To explain their distribution based on chance long distance dispersal is hazardous and creates more problems than it solves.

Bipolar distributions and affinities with South America imply a past continuity of floras, although attempts have been made to explain this disjunction by long-distance dispersal.

The Cordilleran disjuncts in eastern North America are considered to be fragments of the continuous flora; the time of the continuity is uncertain.

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